The Population Ecology of the Nile crocodile (*Crocodylus niloticus*) in the Panhandle Region of the Okavango Delta, Botswana.

by

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DECLARATION

I, the undersigned, hereby declare that the work contained in this thesis is my own original work and that I have not previously, in its entirety or in part, submitted it at any other university for a degree.

Signature: ……..

Date: ……...

ABSTRACT

The Okavango Delta, Botswana, is a unique ecosystem and this is reflected in its extraordinary biodiversity. The Nile crocodile (*Crocodylus niloticus* Laurenti) is the apex predator, and performs a number of vital functions in this system, making it a keystone species. The panhandle crocodile population has declined significantly over the last 80 years and is now threatened as a result of past over-exploitation and present human disturbance. In order to effectively conserve this species and in turn the health of this important region it is imperative to gain an understanding of their ecology and population dynamics.

The population status of the Nile crocodile in the panhandle region of the Okavango Delta, Botswana, was assessed using a combination of capture-mark-recapture surveys, spotlight surveys and aerial surveys. The capture-mark-recapture experiment was conducted continuously from 2002 - 2006. A total of 1717 individuals, ranging in size from 136 mm – 2780 mm SVL, were captured, of which 224 animals were recaptured. Using a Bayesian technique, the total annual population in the panhandle region of the Okavango Delta was estimated to be 2 570 ± 151.06 individuals, with an adult population of 649.2 individuals with the number of breeding females estimated to be 364 individuals. It was concluded that this population cannot sustain the further harvest of breeding animals prior to the increase and stabilization of the population.

Spotlight counts revealed a decline in the encounter-rate of crocodiles on the Okavango River with time, although more long-term data needs to be collected to confirm this trend. During the low-water season (September - February), 22.34 % of all crocodiles were observed, while during the flood-season only 13.34 % were observed, yielding correction factors for spotlight surveys of 4.46 (low-water) and 7.49 (high-water) for all animals in the panhandle.

Two aerial surveys, conducted at the low-water and high-water peaks yielded total estimates of 588 (77.7 % of adults) during the low-water period and 350 (56.7 % of adults) during the high-water period. Correction factors of 1.28 (low-water) and 1.77 (high-water) were calculated for aerial surveys.

An annual average of 50 nests was located in the panhandle, representing a 50 - 60 % decrease over the last 20 years. In regions with high human disturbance, breeding females situated their nests in hidden locations, away from accessible channels.

Hatchlings exhibited elongation of the jaw in order to capture smaller prey items and morphometric shifts in jaw shape coincided with a dietary change at 400 mm SVL. The jaw became broader and deeper as animals matured, presumably in preparation for larger mammalian prey. The average growth rate of recaptured yearlings was 0.198 ± 0.116 $mm.d^{-1}$ SVL and was closely correlated to the amount of time an individual spent in above-average water temperatures. Body condition (RCF) was significantly and positively correlated with a rise in water-level and negatively correlated to time spent in above-average water and air temperatures. Average RCF values were intersected when animals had spent 50 % of their time in above-average temperatures and water level.

Generally crocodiles in the panhandle showed no significant sex-related differences in their sizes or the distances they travelled. The majority of recaptures (62.5 %) moved less than 500 m from the initial capture site. Adults in the panhandle occupied definite ranges, within which were preferred core areas where the majority of their time was spent.

The panhandle crocodile population has declined significantly over the last 80 years, and is now threatened as a result of past over-exploitation and present human disturbance. The management of this population, including both its conservation and sustainable commercial utilisation, requires an adaptive strategy based on accurate monitoring procedures.

OPSOMMING

Die Okavango Delta in Botswana is ‘n unike ekosisteem en word gereflekteer in dié sisteem se buitengewone biodiversiteit. Die Nyl krokodil (*Crocodylus niloticus* Laurenti) is ‘n hoeksteen spesie in hierdie sisteem, maar dié populasies het betekenisvol afgedaal die afgelope 80 jaar. Om hierdie spesie en die gesondheid van hierdie belangrike streek te bewaar is dit noodsaaklik om hul populasie dinamika te verstaan.

Die populasie status van die Nyl krokodil in die pansteel streek van die Okavango Delta, Botswana, was geasseseer deur gebruik te maak van ‘n kombinasie van vang-merk-hervang opnames, kolig opnames en opnames van die lug. Die vang-merk-hervang experiment was op ‘n konstante basis gemonster gedurende 2002 - 2006. ‘n Totaal van 1717 individue wat opeengevolg het in grootte van 136 mm – 2780 mm SVL, was gevang, waarvan 224 diere hervang was. Deur gebruik te maak van die Bayesian tegniek word die totale jaarlikse populasie van die pansteel streek van die Okavango Delta geskat by 2570 ± 151.06 individue. Hierdie sluit ‘n volwasse populasie van 649.2 individue in, met 364 telende wyfies. Die gevolgtrekking is dat die populasie nie verdere oes- of teel-diere kan steun vroër as die toename en stabilisering van die populasie nie.

Kollig tellings wys ‘n afname in die ontmoetings-skaal van krokodille van die Okavango Rivier met tyd. Meer lang-termyn data word egter benodig om hierdie koers te bevestig. Gedurende die laag-water seisoen (September - Februarie), was 22.34 % van alle krokodille opgemerk, terwyl gedurende die vloed-seison was net 13.34 % opgemerk, wat korreksie faktore van 4.46 (laag-water) en 7.49 (hoog-water) vir al die diere in die pansteel streek toegee.

Twee opnames van die lug, gemonster by laag-water en hoog-water pieke het ‘n totale skatting van 588 (77.7 % van volwasse diere) gedurende die laag-water tydperk en 350 (56.7 % van volwasse diere) gedurende die hoogwater tydperk toegegee. Korreksie faktore van 1.28 (laag-water) en 1.77 (hoog-water) was gereken vir opnames van die lug.

‘n Jaarlikse gemiddeld van 50 neste was bepaal in die pansteel, wat ‘n 50 - 60 % afname gedurende die afgelope 20 jaar verteenwoordig. In streke van hoë mense

versteuring, het telende wyfies hul neste in versteekte lokasies weg van bekombare kanale geplaas.

Die brooisels het verlengde kake ontwikkel sodoende om kleiner prooi items te vang, en morfometriese verskuiwing in kaak vorm het gepaartgegaan met ‘n dieets verandering van 400 mm SVL. Die kaak het breër en dieper geraak soos die dier groter geword het, klaarblyklik in voorbereiding vir groot soogdier prooi. Die gemidelde grooi tempo van hervange jaarlinge was 0.198 ± 0.116 $mm.d^{-1}$ SVL en was nouliks gekoreleer met die hoeveelheid tyd wat ‘n individu spandeer het in bo-gemidelde water temperature. Liggaams kondisie (RCF) was betekinisvol en positief gekoreleer met ‘n toename in watervlak en negatief gekorelleer met tyd gespandeer in bo-gemidelde water en lug temperature. Gemidelde ligaams kondisie waardes het gekruis toe die diere 50 % van hulle tyd in bo-gemidelde water temperature en watervlakke spandeer het.

Oor die algemeen het krokodille in die pansteel geen betekenisvolle sex verwante verskille gewys in hulle grootte of die afstande beweeg. Die meerderheid van hervangde krokodille (62.5 %) het minder as 500 m beweeg van die oorspronklikke vang area. Volwasse krokodille in die pansteel het bepaalde gebiede bewoon, waarin daar sekere kern streke was waar die meerderheid hul tyd spandeer het.

Die pansteel krokodil populasie het afgeneem oor die afgelope 80 jaar, en word nou bedryg as gevolg van uitbuiting in die verlede en huidige mense versteurings. Die bestuur van hierdie populasie, insluitend sy bewaring en volgehoue komersiële gebruik benodig ,n aanpasbare strategie gebaseer op akurate moniterings stelsels.

The ultimate value of a crocodile
lies not in his bellyhide,
nor his value as a tourist attraction,
nor even in his ecological significance,
but simply in the fact that he is a crocodile:
big and ancient and monstrously magnificent.

James Powell: IUCN Crocodile Specialist Group, 1971.

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A REVIEW OF SCIENTIFIC STUDY FOCUSING ON THE NILE CROCODILE *CROCODYLUS NILOTICUS* (LAURENTI) IN AFRICA.

1.1 STUDY ANIMAL

1.1.1 Crocodilians: History, evolution and role in the ecosystem

Fossil remains of primitive crocodilians, of thecodont ancestry, appear in the Upper Triassic period some 200 million years ago. In this era, the extinct thecodonts, the dinosaurs, the pterosaurs, or flying reptiles and the ancestors of the birds (Gatesy *et al.*, 2003) were also coming into their own (Bellairs, 1987). Crocodilians of the most advanced kind, the Eusuchians, first appeared some 140 to 65 million years ago and the crocodilians of today all belong to this suborder. There are some 23 species (King & Burke, 1989) found throughout the world today, belonging to Family Crocodylidae which is further divided into 3 subfamilies: a) Crocodylinae, b) the Alligatorinae and c) the Gavialinae. Crocodilians exist throughout the tropics and are considered “keystone” species (Thorbjarnarson, 1992) that maintain ecosystem structure and function. These include selective predation on fish species (Cott, 1961; Pooley, 1982b), recycling nutrients and maintenance of wet refugia in droughts (Thorbjarnarson, 1992).

Throughout their range, crocodilian populations are threatened by overexploitation, hunting, habitat loss and pollution (Thorbjarnarson, 1992). Many species worldwide are exploited for their skins and many populations are threatened due to hunting for trade. The crocodile skin trade generates an international income of $ 500 million annually (Ross, 1998). Crocodile ranching and farming has the potential to harm populations if it is not managed correctly, taking into account population status and demographic trends, and releasing a proportion of wild-originated juveniles back into the systems from which they came. The loss of any species of crocodilian would represent a significant loss of biodiversity, economic potential and economic stability (Ross, 1998).

1.1.2 Ecology

Crocodilians are long-lived animals with very high mortality rates in their first year of life due to predation. They are without exception the largest predators in their aquatic environments and terrestrial mammals, including humans and livestock, fall victim to the larger individuals. Crocodilians exhibit indeterminate growth, and *adult male* Nile crocodiles can *attain* a length of 5 m, although adults average 2.8 - 3.5 m in length (Alexander & Marais, 2007).

They can tolerate a broad range of habitat types including small brackish streams, fast flowing rivers, swamps, dams and tidal lakes and estuaries (Leslie, 1997). Crocodiles are ectothermic animals, regulating their body temperature behaviourally by moving between sun-exposed sandbanks and the water.

Nile crocodiles exhibit a variety of vocalizations from hatchling and juvenile distress signals to adult vocalizations (in defence of young, territories, during copulation or courtship), including jaw-snapping, hissing, bubble-blowing and growling and territorial "roaring" and "bellowing" (Modha, 1967; Pooley, 1982b). Courtship displays involve a number of vocal (female only) and non-vocal (physical) displays (Modha, 1967; Pooley, 1982b). Male-male competition for mates can result in physical confrontation and death of sub-dominant males when the ritual displays of dominant males are ignored (Pooley, 1982b).

Sexual maturity is reached by females over a fairly large size range and is locality-dependent. In the Okavango region, they reach sexual maturity at 232 cm total length (Detoeuf-Boulade, 2006). Wild females reproduce every two to three years (Graham, 1968; Lance, 1989; Kofron, 1990; Guillette *et al.*, 1995), while males are capable of reproducing every year. Nile crocodiles are oviparous pulse breeders and nest in summer at the end of the dry season, when sandbanks are exposed and daily temperatures are at their highest (Cott, 1961; Blomberg, 1976; Pooley, 1982b; Kofron, 1990). In Southern Africa nesting and incubation is between September and January (Pooley, 1982b; Hartley, 1990; Kofron, 1990). The nests are located near permanent fresh water, which the attendant females require to escape from danger and to cool down while remaining close to the nest (Pooley, 1982b). The nest cavities are excavated in a range of substrates, from clay to course-grain, pebbled river sand, after which the eggs (40-80)[1] are laid in the chamber and then covered with sand and incubate for an average of 90 days (Cott, 1961; Graham, 1968; Pooley, 1969; Blomberg, 1976).

Female Nile crocodiles guard their eggs for the duration of incubation (Pooley, 1969; Hutton, 1984) and briefly post-hatching, often not feeding during this period. Breeding therefore represents a large physiological investment on breeding females and may be the reason why wild females do not breed every year, whereas farmed animals do. Although defence of the nest becomes aggressive when the site is approached too closely and as Pooley (1982b) described it

[1] The number of eggs in a clutch ranges considerably, dependent on the length of the female and availability of resources. The average clutch size from Lake Kariba, Zimbabwe is 45 Blake, D.K. & Loveridge, J.P. (1975). The Role of Commercial Crocodile Farming in Crocodile Conservation. *Biological Conservation*, **8**, 261-272., but ranges from 20 - 90 (Departmental records, Department of National Parks and Wildlife Management, Harare - cited in Games, 1990)

"This behaviour succeeds in putting a human intruder to flight". However, this is not always the case and females may abandon nests if they are disturbed by human intruders (Kofron, 1989). Abandoned nests are routinely predated by many species, primarily the Water monitor, *Varanus niloticus* (Pooley, 1982b; Kofron, 1989; Trutnau & Sommerland, 2006), which may be responsible for the predation of up to 50 % of nests. In Australia, approximately 25 % of *C. porosus* eggs usually hatch in the wild due to predation and flooding (Webb & Manolis, 1993).

Along with several other reptile species, crocodilians exhibit temperature-dependent sex determination (TSD). There are no sex chromosomes and the sex of the hatchlings is determined by the incubation temperature during the middle trimester of the incubation period. This has potentially large-scale effects on population sex-ratios. Leslie (1997) discovered that an alien plant, *Chromolaena*, had invaded nesting sites in St. Lucia, Kwazulu-Natal and this was shading the nests, causing a female bias in the hatchlings. Global warming could potentially also advance at a rate faster than these animals can adapt to rising temperatures, leading directly to male-biased populations initially, followed by extinction in a worst-case scenario. The incubation temperature of the clutch does not only affect gender, but also the probability that embryos will survive to hatching, growth rates before and after hatching and the probability of hatchlings surviving to two years of age (Hutton, 1987b; Webb & Cooper-Preston, 1989). The selective advantage of TSD is that it assigns maleness to embryos with high probabilities of surviving and good potential for post-hatching growth (Webb & Cooper-Preston, 1989). In the Okavango, Maciejewski (2006) found that Nile crocodiles exhibited a typically female-male-female (FMF) pattern, a pattern consistent with the production of females in suboptimal environments. Crucial temperatures appear to be between 28.0 – 31.7 ^{o}C for females and 31.7 – 34.4 ^{o}C for males, with females being produced above the upper limit for males (Leslie, 1997; Webb, 1987). Hutton (1987) found that incubation temperature of 31 ^{o}C produced a majority of females and a range between 31.0 – 34 ^{o}C produced males. The FMF pattern of TSD has been documented in *C. niloticus, Alligator mississippiensis, C. johnstoni, C. porosus* and *C. palustris* (Lang, Pers. comm., 2002 – cited in Maciejewski, 2006). In the Okavango Delta panhandle, the lower and upper pivotal temperatures within which males were produced were 31.4 – 33.4 ^{o}C. Maciejewski (2006) describes TSD in more detail.

1.1.3 General status in Africa

Three species of crocodilians occur in Africa, the slender-snouted crocodile (*Mecistops cataphractus*), the Dwarf crocodile (*Osteolaemus tetraspis*) and the Nile crocodile (*C. niloticus*)

(Figure 1). Of these three species, the Nile crocodile is the only one to have established itself in the eastern half of the subcontinent (Blake & Jacobsen, 1992).

Wherever crocodiles come into contact with humans, with the exception of ecotourism and well-managed ranching operations, interaction is negative and ultimately harmful to the crocodiles. Crocodile populations have been drastically reduced or extirpated throughout most of the former areas where these animals occurred, due to eradication programs or commercial hunting endeavours (Thorbjarnarson, 1992). Results of an assessment of *C. niloticus* populations in Africa revealed that populations occur in 42 African countries (Figure 2), of which only 20 populations have been scientifically assessed. The results of these assessments were outlined in Thorbjarnarson (1992) and Ross (1998). Ross (1998) recognized an urgent need for comparative research on population dynamics to be done in central and West Africa. Overall, the Nile crocodile as a species is not threatened and is categorised as "Lower Risk" in the 1996 IUCN Red list (Ross, 1998), as populations may be threatened in some parts of its range. Nile crocodiles were hunted in the 1930's, after which widespread eradication programs were implemented in the early part of the century, carrying on into the 1950's and 1960's (Cott, 1961; Parker & Watson, 1970). Wholesale slaughter of crocodiles abated with the intervention of international legislation by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), which lists the Nile crocodile on Appendix II in Botswana, Ethiopia, Kenya, Malawi, Mozambique, South Africa, Tanzania, Zambia and Zimbabwe (Ross, 1998; CITES, 2007). In all other countries where they occur they are listed as CITES Appendix I (Angola, Bennin, Burkina Faso, Burundi, Cameroon, Central African Republic, Chad, Congo, Cote d'Ivoire, Democratic Republic of Congo, Egypt, Eritrea, Equatorial Guinea, Gabon, Gambia, Ghana, Guinea, Guinea Bissau, Liberia, Madagascar, Mali, Mauritiana, Namibia, Niger, Nigeria, Rwanda, Senegal, Sierra Leone, Somalia, Sudan, Swaziland, Togo and Uganda) (Ross, 1998). A species-level management strategy by the Crocodile Specialist Group, part of the IUCN's Species Survival Commission, also resulted in the reduction of persecution of this species (Thorbjarnarson, 1992). The main threats to the Nile crocodile are conflict with people (Ross, 1998; Combrink *et al.*, in Press), hunting (Cott, 1961; Abercrombie, 1978) and habitat loss and pollution associated with increasing human population density (Cott, 1961; Pooley, 1982a; Thorbjarnarson, 1992; Swanepoel, 1996; Thomas, 2006). Human-crocodile conflict increases as the frequency of encounter does (Combrink *et al.*, in Press) and this conflict invariably results in the reduction of wild populations (Combrink, 2004).

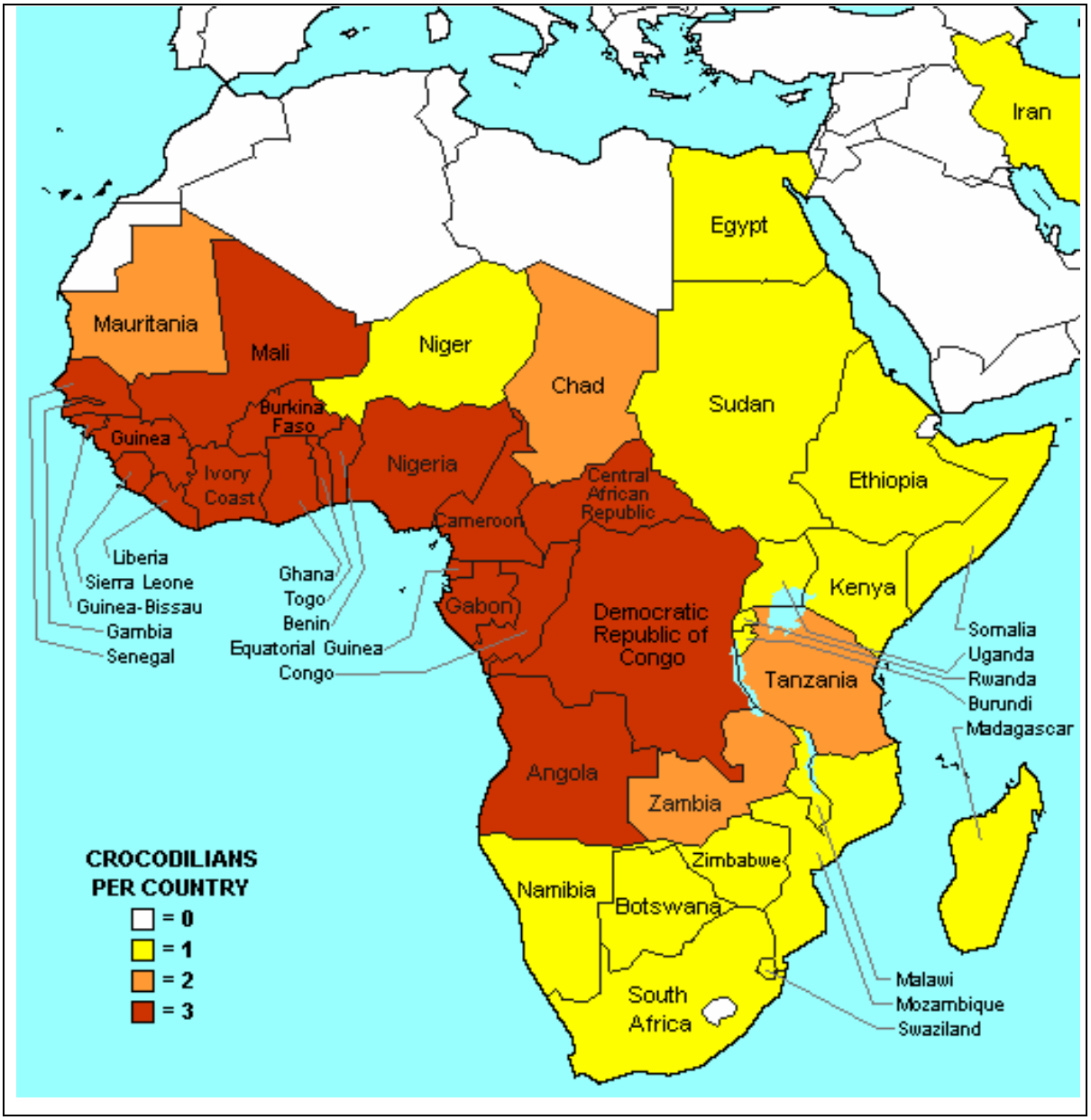

Figure 1. The distribution of the three crocodilian species occurring in Africa, the Nile crocodile (*Crocodylus niloticus*) (1), the slender-snouted crocodile (*Mecistops cataphractus*) (2) and the Dwarf crocodile (*Osteolaemus tetraspis*) (3). (Source: www.flmnh.ufl.edu/cnhc/csl-maps-species.htm, accessed 15/08/07). Note that, although Iran is highlited, this is the Mugger crocodile (*C. palustris*), and not one of the three African species.

Figure 2. The distribution of the Nile crocodile, *C. niloticus*, in Africa and its surrounding islands. Nile crocodiles occur in 42 African countries and range-states.

1.1.4 History of commercial utilization of the Nile crocodile in Botswana

The Nile crocodile population in the Okavango delta has undergone three periods of human-induced decline over the last century. In 1957 the Department of Wildlife and National Parks (DWNP) allowed a quota of 2 000 animals per year to each of two concessionaries. Between 1957 and 1969 an estimated 50 000 crocodiles were shot and trapped by hide-hunters (Pooley, 1982a). It was, however, reported that as many as 80 000 crocodiles could have been destroyed in the Okavango delta during this time (Taylor, 1973) due to losses sustained during cropping operations. Taylor (1973) was informed that 40 000 skins were marketed and remarked that possibly only 50 % of animals shot were recovered. Pooley (1982a) stated that as many as 30 %

of crocodiles may be lost after they are shot, during cropping operations. In 1964 organized hunting ceased and in 1974 all DWNP records pertaining to crocodile hunting disappeared, so harvest figures of recovered crocodiles remain unknown. In 1973 the DWNP set a quota of 500 animals per year for the Botswana Game Industries (BGI) to resume hide hunting. A report generated by Taylor (1973) testified to the fact that there was no population census done prior to the cropping operation and the quota was determined "arbitrarily after due consideration by Game Department personal." In the top 5.6 km of the Kgala Thaoga channel (see Chapter 4, Appendix 2), formerly known as "8 mile Channel", 70 animals (12.5 animals/km^{-1}) were shot in the duration of this operation. In part of the Lower Phillipa channel, a harvest of 6.5 animals/km^{1} (156 crocodiles) was obtained (Taylor, 1973). Taylor's (1973) map of suitable crocodile habitat showed a distinct paucity of crocodiles in the middle of the panhandle, between the entrance to the Upper Phillipa channel and Redcliffs. The quota of 500 animals was filled in 1973, but only 440 crocodiles were shot in 1974 and the venture was hereafter regarded as uneconomic and disbanded. After a decade of no exploitation, farmers removed 1053 live adults and 14 000 eggs from the system between 1983 and 1998 for commercial use in ranching operations. According to the nest survey conducted in 1987 by DWNP, this led to an estimated 50 % reduction in the breeding population (Simbotwe & Matlhare, 1987). In 1988 the total crocodile population was estimated to be 10 000 adults as the result of an aerial survey conducted by Simbotwe (1988).

1.1.5 The conservation genetics consequences of the overexploitation in the panhandle population

In theory, small, isolated populations face a much higher risk of drastic reduction or extinction through stochastic processes as they are not usually as buffered by allelic diversity or heterozygosity as a larger population would be against the effects of genetic drift or selection (Frankham, 2002). It is therefore necessary to monitor the levels of genetic diversity within a threatened population. The removal of eggs and adults from this already overexploited population, without the release back into the wild or immigration of new animals, has potentially dire consequences in this system. In a study investigating the effective population size of the panhandle crocodile population, it was found that moderate levels of heterozygosity had been maintained throughout the periods of exploitation, despite the specific targeting of adults (Bishop *et al.*, in Press). The authors also suggested that the longevity and delayed sexual maturity of Nile crocodiles may have acted to buffer the expected effects of hide-hunting and the removal of breeders for farming purposes (i.e. reduced heterozygosity). However during this period (~ 80 years) the effective population size (N_e) of the panhandle crocodiles underwent a five-fold reduction. Parental generation N_e has decreased from ~ 480 individuals to a current estimate of ~ 90 individuals (Bishop *et al.*, in Press). This result suggested an increased susceptibility for this

population in terms of continuing decline as a function of genetic drift and selection, which results from low population size rather than a lack of heterozygosity (Bishop *et al.*, in Press). At the current effective population size, allelic diversity and heterozygosity will continue to decline through time due to the effects of genetic drift (Bishop *et al.*, in Press). The minimum N_e required to maintain sufficient genetic variation to allow a population to persist through stochastic events varies between species, depending on their life-histories (Bishop *et al.*, in Press). It is generally accepted that maintaining > 90 % of allelic variation will ensure a populations persistence (Spielman *et al.*, 2004). Therefore, to maintain > 90 % of the current allelic diversity and heterogeneity over the next 100 years, it was suggested that an effective (stable) population of at least 150 animals would be required. This equates to a total population of 4200 animals and an adult population of approximately 1060 individuals (Bishop *et al.*, in Press).

1.1.6 Assessing Nile crocodile population status

Nile crocodiles occur in a wide range of habitat types and their behaviour may vary accordingly. Management strategies must therefore be based on local scientific knowledge of the population to be managed. Incorrect estimates of maximum sustainable yields (MSY), for example, can very quickly drive a population to extinction (Magnusson, 1995). The most crucial information required for effective population management is the accurate estimate of population size (Chabreck, 1966), especially where harvesting strategies seek the maximum sustainable yield (Caughley, 1977; Graham, 1987; Woodward & Moore, 1993). Information on population structure, distribution and movements should also be included when management strategies are being decided upon (Norton-Griffiths, 1978). In KwaZulu-Natal, as early as 1971, the Natal Parks Board began conducting surveys to assess the status of the crocodile population. In 1994, an official monitoring program was started (Bourquin & Blake, 1994) to coordinate efforts in the province using aerial and ground survey methods.

Crocodiles are cryptic and rely on their ability to remain undetected for food acquisition and predator avoidance. As such, they are very difficult to census without detailed knowledge of their habits and habitat, good access into the areas they occupy, good equipment and experience. In addition, they are long-lived animals and crocodilian studies should be conducted over a time period sufficient to collect useful data to address ecological and management issues (Bradshaw *et al.*, 2006; Letnic & Connors, 2006). Crocodilian surveys require large investments of time and money. Survey methods must therefore be carefully selected and designed to maximize efficiency, accuracy and precision (Thomas, 1997; Stirrat *et al.*, 2001).

I Nesting ecology

Pooley (1982b) found that areas with the highest crocodile densities were also those with the highest nest densities. A number of useful estimates can be calculated using nesting surveys. if the proportion of mature females in the population is known and the proportion of mature females actually nesting is known[2], an estimate of total population can be calculated (Games, 1990). Leslie (1997) estimated nest effort for the Lake St. Lucia population based on a total population estimate. This information obviously has important ramifications for the management of the population as a whole. A population monitoring program for the Okavango region, based on the number of nests detected through aerial photography was suggested based on the assumption that all nests would be visible from the air and that the number of nests would directly correlate to the number of crocodiles (Graham *et al.*, 1976). Taylor (1973) noted that the stretch of river entering Botswana, while offering optimal nesting habitat, was even then ignored due to the presence of people and domestic animals. Taylor (1973) conducted a survey covering approximately 20 % of the area in which they cropped (i.e. shot animals) and located 15 nests. Two of the nests had been predated by local people and Taylor was told upon enquiry that the eggs were taken for food (Taylor, 1973). In a total of 18 clutches (13 from nests and 5 from dead female breeders), Taylor (1973) found an average of 63 eggs per clutch. Taylor (1973) then calculated recruitment into the total population based on nest densities and clutch sizes. This proved dangerous in terms of managing the population, as the resulting quotas were too high and cropping was abandoned the following year due to insufficient numbers of crocodiles.

II. Crocodile growth

The correlation between crocodilian age and size may be one of the most fundamental life history traits (Webb & Smith, 1987) because it allows age, maturity and senescence to be estimated. However, in large ectotherms, demographic parameters are poorly related to age and growth is a primary interest as life-history phenomena are related to body size (Peters, 1983; Hutton, 1987a). Crocodilian growth rates are typically very variable, especially in the hatchling, yearling and juvenile size classes (Cott, 1961; Blake & Loveridge, 1975; Webb *et al.*, 1978; Hutton, 1987c; Kay, 2004b), and between populations at a geographical scale. Captive crocodilians under optimal pen densities, feeding and temperature conditions, will grow faster than those in the wild (Hutton, 1987c), sometimes doubling “natural” growth rates (Chabreck & Joanen, 1979). It is difficult to assign ages to wild crocodiles after only 3 - 4 years of growth

[2] Female crocodiles may not breed every year. Kofron, C.P. (1989). Nesting Ecology of the Nile crocodile (*Crocodylus niloticus*). *African Journal of Ecology*, **27**, 335-341.

(Cott, 1961; Webb *et al.*, 1983; Hutton, 1984). Different size classes also exhibit differing growth rates, with the growth rate to size relationship changing at 4 - 5 years of age (Hutton *et al.*, 1987). Webb *et al*., (1978) found that a linear growth pattern was exhibited for *C. porosus* up to 800 mm snout-vent length (SVL), but that this fitted line did not describe the growth rates for larger animals. Smaller animals tended to have a much higher relative length-related growth rate than larger animals, whereas larger animals increased at a relatively higher rate in terms of mass. Growth rate data for the particular population under study are therefore required to make local management decisions (Hutton, 1987c; Wilkinson & Rhodes, 1997).

Due to the high cost of equipment and the challenging logistics involved when working in an aquatic environment, there is little available long-term data on crocodilian growth rates in the wild.

Seasonal changes also have a significant influence on crocodilian growth. Ambient temperature plays an important role in growth (Hutton, 1987a) where sub-optimal temperatures can cause lower feeding and digestion rates. Many juvenile alligators actually “shrink” during the cooler period of the year (Chabreck & Joanen, 1979), decreasing by 1.0 mm - 4.0 mm in total length per month.

In addition to ambient temperatures, fluctuating water levels have a profound effect on the distribution and behaviour of wild crocodile populations (Pooley, 1982b). Seasonal flooding allows crocodiles to exploit new habitats and food sources and this, combined with warm weather, normally results in increased growth rates (Webb *et al.*, 1978; Hutton, 1987a). This is the case in the Okavango panhandle, where annual flooding follows the rainy season and the seasonal floodplains are inundated with water.

III. Movement patterns

Animal movement patterns need to be assessed to understand basic population processes and can themselves be important demographic processes (Hutton, 1989). Dispersal is the movement of individuals away from the area in which they spent the initial part of their lives (Hutton & Woolhouse, 1989). Innate dispersal is spontaneous, genetically determined and generally random whereas environmental dispersal is often short and directional resulting from the avoidance of unfavourable habitat or social conditions.

A. Demographic movement

Most crocodilians show low spatial movement patterns throughout their lives (Webb & Messel, 1978; Magnusson, 1979; Webb *et al.*, 1983; Hutton, 1989; Tucker *et al.*, 1997a; Tucker *et al.*, 1997b; Tucker *et al.*, 1998; Munoz & Thorbjarnarson, 2000) and these are primarily associated with life-history stage and gender (Kay, 2004a). To reduce conflict or cannibalism there may be movement or segregation of individuals based on size-dependent prey differentiation (Hutton, 1984; Letnic & Connors, 2006). In Lake Ngezi, Hutton (1984) found that animals smaller than 220 cm had home ranges that were small and localized. Dispersal of animals away from the nesting areas occurred at around 120cm total length. Juvenile animals moved mostly in summer, ranging significantly further than in winter. Separation of juveniles from adults appeared to be ecological (Cott, 1961; Pooley, 1982b; Hutton, 1989) in nature and may have resulted from the threat of cannibalism.

Animals over 120 cm may have been excluded by adults, where smaller animals were still accepted. Larger crocodiles ranged increasingly widely and the largest non-breeders had no distinct centre of activity. Mature, breeding females typically restricted themselves to nesting areas all year round, had small home ranges and were sedentary. In contrast, Kay (2004b) found that mature *C. porosus* females had a distinct and separate dry-season habitat and moved into the breeding area at the beginning of the rainy season. This difference could be related to the different nesting techniques (mound as opposed to hole) used by the above species. However, Pooley (1982b) also describes the annual exodus of breeding *C. niloticus* from pans to nearby breeding areas along the Pongola River at the start of the breeding season. A similar rise in the number of mature animals in Lake St. Lucia immediately following the breeding season also pointed to distinct and separate breeding and non-breeding home ranges. The data Hutton (1984) collected on large males showed non-overlapping ranges i.e. they are territorial during the breeding season (Cott, 1961; Modha, 1967; Hutton, 1984). Leslie (1997) found that mature crocodiles moved seasonally and from year to year. This movement was influenced by breeding status, salinity, the presence of humans and fish migrations. Radio-telemetry and mark-recapture techniques (Cott, 1961; Hocutt *et al.*, 1992; Leslie, 1997; Swanepoel, 1999; Kay, 2004b; Campos *et al.*, 2005) are two methods used to determine crocodilian movement patterns. Radio telemetry has been used to track *C. niloticus* in Lake Ngezi, Zimbabwe (Hutton, 1989; Hocutt *et al.*, 1992). Other species that have been successfully tracked include *Alligator mississippiensis*, *Crocodylus acutus, C. intermedius, C. porosus, Paleosuchus trigonatus* and *Melanosuchus niger* (Kay, 2004b).

B. Density dependence

The probability of seeing certain animals may depend on population density (Harris, 1986). One example of this may be a population of animals that prefer densely vegetated habitats and are forced into more open habitats with increasing numbers and are thus encountered more frequently. Webb (Pers. comm., 2007) suggested that it could be argued that few if any population parameters are free of density effects. Webb *et al.*, (1987) reported an apparent link between the number of larger crocodiles in the population and the survivorship of 2 – 3 year old *C. porosus.* Letnic and Connors (2006) suggested that subadult male *C. porosus* avoid aggression by larger males by dispersing from preferred habitats with high crocodile densities to peripheral and less favourable habitats such as marine waters. Males move further and more often than females (Webb & Messel, 1978; Kay, 2004a) and are also involved more frequently in aggressive intra-specific displays than females, lending support to the "male dispersal" hypothesis suggested by Letnic and Conners (in press, cited in Letnic & Connors, 2006). While this may be true for populations such as *C. porosus* in Australia, that are approaching carrying capacity, it may not be the case for other less abundant species. Woodward *et al.*, (1987) tested whether competition for nesting space in the American alligator was a density-dependent mechanism and found this not to be the case. Hines & Abercrombie (1987) found that cannibalism in alligators predominantly effected larger juveniles and Woodward *et al*., (1987) reported that survival rates among the youngest alligators may be influenced more by cyclic changes in water levels than by alligator densities.

C. Daily movement: Temperature

Daily movement patterns are generally determined by weather. Crocodiles are ectothermic and regulate their body temperature behaviourally, by alternatively sunning themselves to warm up and then moving into water or shade to cool down. Cott (1961) and Modha (1967) both observed peak basking times before and after the midday heat. Crocodiles are nocturnally aquatic (Pooley, 1982b), although may be found ashore moving between habitats or lying on banks on warm, humid evenings (Pooley, 1982a; Bourquin, Pers. obs.). Crocodiles avoid areas where their basking sites are routinely exposed to wind and wave action (Modha, 1967; Graham, 1968; Pooley, 1982b). Evenings are spent in the water, where body temperature is buffered from the cooler air temperatures and this time is used to hunt. In addition to these daily movements, crocodiles exhibit a seasonal shift in behavioural patterns, tending to spend a great deal more time under water or exposing less of their bodies to the air when it is cold (Smith, 1979). Hutton

(1989) found that juvenile Nile crocodiles moved further in summer than in winter, although the correlation between temperature and adult movement patterns less clear.

D. The effect of water level on movement patterns and encounter rates

The effect of water level on movement patterns, and therefore the rates at which crocodiles are encountered during surveys, is not a new observation (Woodward & Marion, 1978; Messel *et al.*, 1981; Webb *et al.*, 1990; Ron *et al.*, 1998). Short-term changes in water levels associated with tidal shifts, or longer-term changes associated with flooding have a profound effect on crocodilian movement all over the world (Woodward & Marion, 1978; Messel *et al.*, 1981; Messel & Vorlicek, 1987; Games, 1990; Webb *et al.*, 1990). Messel *et al.* (1981) found that large crocodiles that were sighted at high tide moved vertically and horizontally with dropping water-level, and were not necessarily sighted again at low tide (and *vice versa*). Wood *et al.* (1985) found that *A. mississippiensis* also dispersed during high - water seasons. Where the floodplain was narrow, with little adjacent wetland, densities were not significantly correlated with water level (Wood *et al.*, 1985). Crocodilians moved out of survey areas into the surrounding floodplains or wetlands when water levels rose and concentrated in main channels in the dry season. As the more accessible main channels are normally the areas in which surveys are conducted, this seasonal shift affects the number of crocodiles observed. Games (1990) found that crocodiles moved out of his study area in the Ume River towards Lake Kariba when water levels receded in the dry season. Ron *et al.* (1998) found that water level was the most important factor affecting the spatial distribution of crocodilians in the Amazon Basin, with most animals remaining in flooded forests during the rainy season and retreating to the deepest areas of lakes when forced to do so by reduced water levels during the dry season (Ron *et al.*, 1998). Similar tendencies were found in the Pantanal (Coutinho & Campos, 1996). Woodward and Moore (1993) suggested measuring water level during surveys to isolate its effect on crocodilian counts and that surveys should be conducted at the same time every year to limit seasonal variation. Given sufficient funding, surveys should be conducted throughout the year to calibrate seasonal differences for comparative purposes, especially if seasonal movement patterns are being investigated (Combrink *et al.*, in Press).

1.2 SELECTING SURVEY METHODS

The most common methods used to estimate crocodilian population size are diurnal surveys (Gaby *et al.*, 1985) spotlight counts, (Webb & Messel, 1979; Glastra, 1983; Montague, 1983; Bayliss *et al.*, 1986; Hutton & Woolhouse, 1989; Walsh, 1989; Games, 1990; Woodward & Moore, 1993; Pacheco, 1996; Da Silveira *et al.*, 1997; Ron *et al.*, 1998; Platt & Thorbjarnarson,

2000b; Platt & Thorbjarnarson, 2000a; Thorbjarnarson *et al.*, 2000; Stirrat *et al.*, 2001; Brown *et al.*, 2004; Letnic & Connors, 2006), capture-mark-recapture experiments, (Chabreck, 1963, 1966; Parker & Watson, 1970; Graham, 1987; Games, 1990; Jennings *et al.*, 1991; Ramos *et al.*, 1994; Tucker *et al.*, 1997a; Ron *et al.*, 1998; Munoz & Thorbjarnarson, 2000; Cherkiss *et al.*, 2004; Kay, 2004b; Letnic & Connors, 2006) aerial surveys (Magnusson *et al.*, 1978; Magnusson *et al.*, 1980; Bayliss *et al.*, 1986; Games, 1990; Thorbjarnarson, 1992; Ramos *et al.*, 1994; Coutinho & Campos, 1996; Brown *et al.*, 2004; Combrink, 2004; Read *et al.*, 2004) or a combination of these techniques (Graham, 1968; Gaby *et al.*, 1985; Bayliss *et al.*, 1986; Hutton & Woolhouse, 1989; Games, 1994; Combrink, 2004). Hutton and Woolhouse (1989) cautioned against the estimation of total abundance from uncorrected counts, such as aerial survey and spotlight counts, deeming these data inappropriate until corrected for factors such as visibility biases.

Generally, crocodilians show seasonal and size-dependent behavioural (eg. movement patterns) and ecological (eg. size-dependent dietary shifts) differences. Survey methods must take into account both seasonal and geographic variations and survey techniques must account for as many possible sources of variation as possible when estimating population demographics (Letnic & Connors, 2006).

1.2.1 TOTAL COUNTS

Due to their aquatic, cryptic nature and the wide range of habitats crocodiles frequent, total counts are often prohibitively expensive (Bayliss, 1987). The ability to see crocodiles varies temporally and therefore total population counts are rarely, if ever, achieved in the wild (Games *et al.*, 1992; Nichols, 1992). In addition, total counts are unrealistic in large areas such as the Okavango Delta where much of the habitat is inaccessible (Hutton & Woolhouse, 1989). However, this method has successfully been used in small rivers and lakes (Hutton, 1992).

Sample counts involve dividing and total sample area up into more manageable subdivisions, surveying them and then extrapolating for the whole region (Games *et al.*, 1992). Individuals in crocodilian populations are almost never randomly spaced (Combrink, 2004). Rather, crocodiles concentrate in favourable habitats or areas where resources are abundant. Reasons for the spatial distribution of crocodiles may include seemingly insignificant factors such as avoidance of prevailing winds and subsequent wave action (Combrink, 2004). For this reason stratified sampling, which is defined as sampling over a range of habitats within which the population

density is fairly uniform (Caughley, 1977), is commonly used when surveying crocodilian populations (Combrink, 2004).

1.2.2 Capture-mark-recapture methods

The capture-mark-recapture method involves capturing an animal, marking it uniquely, releasing it and recapturing it subsequently (Sutherland, 2006). The proportion of animals recaptured is a function of the total population and population abundance can be calculated using a number of methods (Sutherland, 2006). Hutton and Woolhouse (1989) listed the difficulties of estimating crocodile numbers through capture-mark-recapture experiments as: inaccessibility to some habitats, differing size-dependent behaviour and the difficulty of satisfying the strict assumptions inherent in capture-mark-recapture models.

Capture-mark-recapture techniques assume an equal probability of capturing all individuals, regardless of whether they have been captured before or not. These assumptions are often violated (Bayliss, 1987). For example, Kay (2004b) found that crocodiles that were previously trapped allowed boats to get closer with the spotlight than those that were initially harpooned and that larger crocodiles were more wary than smaller individuals. Taylor (1973) stated of the Okavango crocodiles, “The older and therefore larger, animals are extremely difficult to approach with the noisy outboard motors, splashing of the boat’s wake and the flashing of powerful spotlights.”

In capture-mark-recapture studies, individuals must be unambiguously marked so that they can be individually recognized when recaptured. Crocodilians are traditionally marked by means of scute-removal, the attachment of numbered plastic tags (Bayliss *et al.*, 1986; Hutton, 1989; Games, 1990; Leslie, 1997; Kay, 2004b), the insertion of PIT tags (Kay, 2004b) or a combination of the above. Scute-removal is a permanent marking technique, whereas plastic tags have varying degrees of longevity. The capture-mark-recapture method is one of two recognized manners in which to quantify concealment and diving bias, that together form the highest proportion of visibility bias in crocodilian surveys (Kay, 2004b). This method requires crocodilians to be physically captured and processed. It is expensive and requires more resources (personnel, equipment and time) than other censussing methods. However, the mark-resight method does not require the animal to be recaptured after the initial capture; rather the animal simply has to be positively identified and this qualifies as a “recapture” (Bayliss, 1987). While this may increase the number of “recaptures”, it does not allow the collection of additional morphometric measurements or blood and urine samples. These additional data are usually

necessary for ecological studies, to maximise the data for the effort and expense required to capture the crocodiles.

1.2.3 Spotlight counts

Nocturnal spotlight counts are used throughout the world to evaluate crocodilian population trends (see previous reference listing). Standardised spotlight surveys were first developed by Messel *et al,* (1981) and have been used extensively in Australia since 1971, in several major river systems (Stirrat *et al.*, 2001).

While spotlight counts can provide fairly accurate estimates of abundance, there are many factors that can lead to inconsistent, inaccurate results (Hutton & Woolhouse, 1989). Visibility biases due to vegetation cover, narrow channels, twisting rivers, the position of the crocodile or its wariness, can all lead to under estimates of population (Bayliss *et al.*, 1986). Older animals tend to be more wary and therefore less easily caught than younger animals (Webb & Messel, 1979; Hutton & Woolhouse, 1989) and often submerge when a boat is heard or a spotlight approaches. Additionally, spotlight counts can only work where there is access by boat.

Hutton and Woolhouse (1989) applied correction factors to spotlight count data collected over a period of three years on Nile crocodiles in Lake Ngezi, Zimbabwe. These correction factors were obtained from capture-mark-recapture data collected over the same period. Between 10 % and 62 % of the total population was observed during spotlight counts, with a mean of 36 ± 13 % throughout the entire study. On an average night in Louisiana, only approximately 25 % of all adult alligators were sighted (Taylor & Neal, 1984). Hutton and Woolhouse (1989) suggested that sightability was most affected by water level, which counted for 61 % of the variation in the total numbers seen. They calculated that up to 37 % of the crocodiles in Lake Ngezi were under water (diving bias) during their surveys, a similar result to the estimate of 38 % calculated by Bayliss *et al.* (1986) for *C. porosus*. Unfortunately it is only possible to calculate diving bias' when absolute abundance is known (Bayliss *et al.*, 1986; Graham, 1987; Hutton & Woolhouse, 1989). A survey by Bayliss *et al.* (1986) for three different habitat types [wide (100 m) river with few bends, 50 % vegetation cover; narrow (50 m) with many sharp bends, 80 % vegetation cover; very narrow (10 - 20 m) with many sharp bends, 100 % vegetation cover] revealed that 66 %, 59 % and 35 % respectively of all saltwater crocodiles present were detected by spotlight.

Spotlight counts therefore represent an index of the total population. Woodward and Moore (1993) sum it up in the following manner: "Although the exact relationship between a count and the total population (sighting proportion) may be unknown, for trend analysis, we either assume

that this relationship remains constant over time or that we can account for factors affecting the sighting proportion. Thus, any change in counts should reflect a proportionate change in the total population."

The spotlight method is however subject to the least bias of all the methods used to assess crocodilian populations (Hutton, 1992). It was effective at detecting a significant departure of 10 % from a nominated population size of *C. porosus*, within four years. This would allow management strategies to correct these deviations within that generation period of 12 years by adjusting commercial harvesting quotas (Stirrat *et al.*, 2001).

1.2.4 Removal method

If animals in a closed population are cropped, then fewer and fewer animals are going to be encountered as the population declines. When the numbers of animals removed in each successive cropping session are plotted against the total number already removed, this decline will be obvious. The population estimate of the selected size-class will coincide with the point where the x-axis (total animals removed) is intercepted by the extrapolated trend-line that is fitted to the data (Sutherland, 2006). This method can only be used for closed populations, so that no new animals immigrate and replace the cropped crocodiles (Sutherland, 2006). Populations can therefore theoretically be estimated in this way. However, a draw-back of this technique is that estimates are not precise unless a large proportion of the population is removed (Sutherland, 2006). A total removal method was used to derive estimates of real abundance versus relative abundance for Australian freshwater crocodiles in small isolated lagoons (Webb, Pers. comm., 2007).

1.2.5 Aerial surveys

Aerial surveys are useful for surveying inaccessible or large areas, but vary widely in their success (Pooley, 1982b). Caughley (1977) found that 12 % - 61 % of animal populations were not observed during aerial surveys. Depending on habitat types and observer bias, up to 88 % of crocodiles may not be detected from the air during surveys (Ramos *et al.*, 1994). Crocodiles are cryptic and aquatic and therefore individuals less than 2 000 mm in total length are not easily seen (Parker & Watson, 1970). This is exacerbated by dirty or turbid water, the presence of vegetation or reflection of the sun off the water surface. The type of aircraft used is an important factor in the percentage of animals seen.

Fixed-wing aircraft provide the space necessary for multiple observers but are difficult to manoeuvre and cannot hover or reach the very slow speeds of various other types of aircraft,

such as ultralights or helicopters. Fixed-wing aircraft have, however, been used successfully to count Nile crocodiles (Graham, 1968; Leslie, 1997). Pooley (1982a) found that a helicopter provided slow cruising speeds, safe low-altitude flying and the ability to manoeuvre with twisting rivers and streams when counting crocodiles. Helicopters also have the ability to hover when a group of animals is seen so that they can be counted and / or photographed. In addition, helicopters offer a wider field of view than standard aeroplanes. However, despite this, helicopters are very expensive to run and maintain. Helicopter surveys in Australia showed no significant correlation to spotlight counts in a study on *C. porosus*, sometimes even correlating negatively with the spotlight count data (Stirrat *et al.*, 2001). In addition, it was reported that helicopter survey data would take a much longer time to detect population trends (Stirrat *et al.*, 2001) and would not be able to detect trends in declining populations within the time constraints required for effective management (in this case, within half a generation, or 6 years). However Webb (Pers. comm., 2007) explained that the major variation in the helicopter counts reported in Stirrat *et al.* (2001) came from two years in which different observers were used, particularly Stirrat himself in the last year, without any calibration against the previous observer, who saw about 30 % less (observer error). This introduced huge variation into the counts, increasing the time it would take to detect a change. Webb (Pers. comm., 2007) communicated that helicopter counts in Western Australia are continuing to provide an accurate and precise method of tracking trends in the population over 20 years.

An ultralight has the advantage over other, larger fixed-wing aircraft of being able to fly safely at much lower altitudes, at much lower speeds, thus giving observers more time to observe individuals (Coutinho & Campos, 1996; Combrink, 2004; Botha, 2005). High survey speed can cause an observer to miss animals, whereas low speeds can lead to double-counting of animals at high densities (Combrink, 2004). In addition, a low counting rate can result in a high accuracy and also the counting error may increase with counting rate (Norton-Griffiths, 1978).

1.2.6 Nesting surveys

Nesting sites are usually located by boat or on foot, sometimes subsequent to aerial surveys (Pooley, 1982a; Graham, 1987; Combrink, 2004). Aerial surveys can be important when nests are located away from the main channels to locate sites and to determine the best routes to get to them on foot. This can be especially important in areas like the Okavango Delta, where a maze of waterways is usually surrounded by dense stands of Papyrus and *Phragmites* stands. This holds true when females hide their nests away from readily accessible channels when in disturbed areas (Combrink, 2004). Combrink (2004) conducted nesting surveys on foot and by motor bike. Generally, to locate nest sites the observers look for well used “slides” used by the

female crocodile to approach and leave the nest site (Chabreck, 1966) from the river. Often the female will use one path out of the river and another (usually a more direct route) back to the nearest water, especially when the bank is high (Pers. obs.; Pooley, 1982b). Pooley (1982b) found that in a system with periodic flooding, the height of the nest site above water was the primary factor in its location.

A list of nesting surveys conducted to census *C. niloticus* populations within southern Africa follows:

1. Modha (1967) - Lake Rudolf, Kenya
2. Pooley (1982b) - Ndumu, Mkhuze and St. Lucia game reserves (KwaZulu-Natal, South Africa)
3. Graham *et al.*, (1976) - Okavango River (Botswana)
4. Kofron (1989) - Chipinda pools (Zimbabwe)
5. Games (1990) - Lake Kariba (Zambia) and Cahora Bassa (Mozambique)
6. Leslie (1997) - Lake St. Lucia (KwaZulu-Natal, South Africa)
7. Swanepoel (1999) - Olifants River, Kruger National Park (Mpumalanga, South Africa)
8. Combrink (2004) - Lake Sibiya (KwaZulu-Natal, South Africa)
9. Botha (2005) - Flagship Boshielo Dam (Mpumalanga, South Africa)
10. Aust (present) - Namibia

1.3 MODELLING POPULATION DYNAMICS

The 1980's saw a shift in emphasis away from estimating the number of animals in a population using Jolly-Seber models (Jolly, 1965; Seber, 1965) in which mark-recapture data were collected (Lebreton *et al.*, 1992). Rather, emphasis was placed on estimating population survival and capture rates (Lebreton *et al.*, 1992; Schwarz & Arnason, 2005) using Cormack-Jolly-Seber models (Cormack, 1964; Jolly, 1965; Seber, 1965). This shift was advantageous because survival estimators are a great deal more robust to the partial failure of assumptions than were estimators of population size (eg. assumption of homogeneity of individuals to capture or recapture) (Lebreton *et al.*, 1992). When estimating survival rates, a random mixing of marked individuals is not necessary and this is only the case when estimating population size (Lebreton *et al.*, 1992). However, when estimating population size, capture design can induce independence of individuals and equality of rates of capture when mixing is not random (Lebreton *et al.*, 1992) by using random routes across a study area.

The improvement and increased power of computing software allowed various complex models to be fitted to data and then compared using goodness-of-fit and likelihood ratio tests (Cooch,

2001). The models allowed for the testing of biological hypotheses by applying meaningful constraints and covariates to the data, thereby better understanding biological processes responsible for driving population dynamics. Knowledge and understanding of the population under study is still a requirement with these methods as it drives the selection of the appropriate class of models on which to base data analysis - while some models may fit the data, they make no sense biologically. This knowledge combined with enhanced computing power (Franklin, 2001) allows one to model population dynamics by grouping individuals for analysis according to their categorical variables (sex, age, etc) or based on individual continuous covariates (mass, age / size, body condition), which need to be taken into account in modelling survival (Lebreton *et al.*, 1992). In these models, the program MARK uses a general linear model approach as the basis for all analysis types possible (Cooch, 2001).

1.4 SYNTHESIS

Crocodiles are extremely difficult animals to census. Ideally, long-term studies should be conducted to gain an understanding of the population in question. A clear understanding of the fundamental questions that the research is attempting to answer must be gained before the survey technique is selected. While aerial and spotlight techniques give insight as to population trends and indices of population status, these need to be done with an idea of the error associated with each technique, which can then be corrected for. Various factors affecting the proportion of animals that are visible and observed, such as observer bias, seasonal variation, water-level fluctuations and habitat type, to name but a few, are best analyzed with long-term data-sets. Mark-recapture techniques are the most reliable methods with which to estimate population size, always paying careful attention to the design of the surveys and the assumptions of the models being applied. Again, long term data is necessary to gain an understanding of factors affecting the densities of crocodiles.

1.5 STUDY SITE: A GENERAL DESCRIPTION OF THE PANHANDLE AND OKAVANGO DELTA.

The Republic of Botswana, which is entirely landlocked and bordered by South Africa, Zambia, Zimbabwe and Namibia, occupies a huge chunk of Southern Africa. The countries' game areas are among the finest in the world and include the well known Okavango Delta (Figure 3). The Okavango Delta is the Worlds largest Ramsar site[3] (Ringrose, 2003; Swatuk, 2003). The Okavango Delta is a very unique and fragile ecosystem, providing high-quality habitat for

[3] The RAMSAR Convention is the Convention on Wetlands of International Importance which provides the framework for international cooperation for the conservation of wetlands, the first and, so far, the only ecosystem type which has its own international treaty. The parties to the convention agree to include wetland conservation in their national planning and to promote their sound utilization (www.ramsar.org, Updated 12 March 1999. Accessed 7 August 2006).

thousands of mammals, birds, fish, amphibians and reptiles. It also sustains hundreds of thousands of human residents of five ethnic groups and a growing ecotourism industry. Visitors to the Okavango area, account for 80 % of Botswana's tourism which accounted for 4.5 % of Botswana's Gross Domestic Product (GDP) in the year 2000 (Mbaiwa, 2002). The panhandle and its riverine floodplain, together with the upper part of the Delta, forms a permanent swamp while the lower parts of the Delta comprise seasonal floodplains (Mendelsohn & el Obeid, 2004).

While on its ~ 100 km journey through the panhandle, from the Botswana / Namibia border to Seronga Village in the south-east, the Okavango River is wide and fast flowing. The current prevents the advance of vegetation, predominantly papyrus (*Cyperus sp.*), at its edges. Swamp specialists such as hippopotamus, crocodiles and predatory fish live in the main channels, while the papyrus swamp has its own specialized forms of animal life. As soon as the Okavango River leaves the panhandle area, it spreads out over the sands of the Kalahari forming the fan. The northern part of the Delta is characterized by shallow - water, flooded grasslands, backwater swamps, ox-bow lakes and many hidden lagoons mostly interconnected by narrow waterways. A few main channels lined by tall reeds (primarily *Phragmites australis*), carry the remainder of the Okavango's water southwards through the fan, to discharge into the Boteti River when there is sufficient water. Papyrus, which dominated in the Panhandle region is replaced by other reeds (*Pychreus machrostachyus*), sedges and grasses (eg: *Miscanthidium junceum*) in the temporary swamp. Scattered throughout the southern portion of the fan are thousands of islands, 70 % of which are formed through the activities of termites, but that are also formed by various other processes such as aggradation (McCarthy, 2004). Many islands are high enough above the reed beds and floodplains to support the growth of large trees and a diversity of terrestrial animal populations.

Only about one sixth of the land allocated to wildlife in Botswana has the ability to generate high economic value from wildlife utilization. This includes the land around the Okavango Delta, the northern riparian systems and some pans (Barnes, 2001). Most of the Delta's soils cannot support large-scale agriculture because they are low in nutrients and have poor water retention (Mendelsohn & el Obeid, 2004). However, small-scale crop farming of millet, maize and sorghum is practiced and domestic livestock are allowed to graze in the floodplains. Local inhabitants utilize resources provided by the river, such as reeds (*Phragmites sp*), which are cut during low-water season for building purposes and fish, that are caught using nets and by angling. In September and October, fires are deliberately set in the dry papyrus beds of the

panhandle destroying large tracts of vegetation (mainly *Cyperus* and *Phragmites sp*), often in a continuous band from Seronga to Shakawe (Shacks, 2006).

1.5.1 Geology

The Okavango River system lies in the Kalahari Basin, a depression in the interior of Southern Africa (McCarthy, 2004) consisting mainly of wind-blown Kalahari sands. The river is shared by three countries, Angola, Namibia and Botswana and has its origin in the Angolan highlands, about 1700 m above sea level (Cubango catchment). The Cubango River is joined by the Cuito tributary to form the Okavango River, which enters north-eastern Botswana and forms a very broad, linear floodplain known as the panhandle. After encountering the Gumare fault the water contained by the panhandle fans out to form the Okavango Delta proper (Mendelsohn & el Obeid, 2004). The Gumare fault is part of a half-graben fault (McCarthy, 2004) which formed around 200 million years ago and is ultimately responsible for the very low gradient which caused the physical characteristics of the fan-shaped delta. These faults are the result of weaknesses in the earth's crust and are an extension of the East African Rift Valley (McCarthy, 2004).

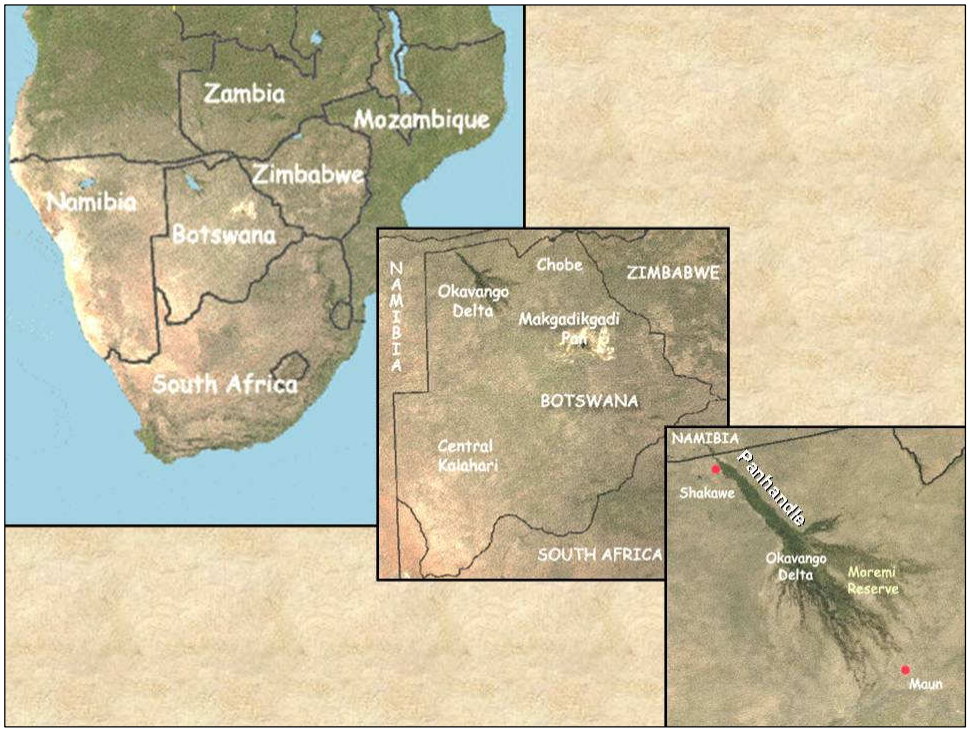

Figure 3. The study area of the Okavango Crocodile Research Group, in the Panhandle region of the Okavango Delta, Botswana.
(source: **http://www.egnu.com/maps/okavango_map.html**, accessed on 28/07/07).

1.5.2 Hydrology

The Okavango Delta (Figure 3) is, strictly speaking, not a proper delta that has, as it's end-point, a standing body of water (McCarthy, 2004). The "delta" is in fact an alluvial fan, with the outflow of water ending its journey in the sands of the Kalahari Desert. The Okavango system has a catchment area of 111 000 km^2, with the fan covering 11 400 km^2 at its peak flood in the last 30 years (Mendelsohn & el Obeid, 2004). At its base flow in the dry season, there is sufficient water to sustain about 6000 km^2 of permanent swamp (McCarthy, 2004). This annual flooding onto the shallow gradient of the fan area, combined with a complex interplay of biotic ecosystem engineers, such as hippopotamus and termites and the dominant aquatic vegetation, drives the whole Okavango ecosystem. The entire system is extremely dynamic, with various channels "drying up" due to aggradations and new channels forming from existing hippopotamus paths and leading into lower lying areas. Due to the dynamic nature of the delta, most channels have a finite existence in the region of about 150-200 years (McCarthy *et al.*, 1988). The annual rains begin in October and continue through to February. Water flow is augmented by rainfall from the Angolan catchments and areas north of Botswana and peaks in the Okavango River at Mohembo in April, having raised the dry-season water level by 1.7 m (McCarthy, 2004). The size and timing of the annual flood depends more on the amount of rainfall in the catchment area than local rainfall (Mendelsohn & el Obeid, 2004). The catchments' area provides some 11 000 million m^3 of water to the delta annually and local rainfall contributes a further 5 000 million m^3 (McCarthy, 2004). The alluvial fan consists of numerous semi-permanent drainage channels, lagoons and floodplains, which link up during the annual flood. Once in the fan, the flood water takes a further four months to reach Maun (Figure 3) in August due to the shallow gradient produced by historic sedimentation. In Maun, water levels may rise by as much as 2.7 m (McCarthy, 2004). Evaporation is three to four times the amount of precipitation due to the semi-arid nature of the area and some 96 % (± 15 400 million m^3) of the inflow into the delta is lost to the atmosphere by evapotranspiration (McCarthy, 2004). For a synopsis on the formation of the Okavango Delta and processes that drive it, see McCarthy (2004).

The Okavango system is a closed system, with all recruitment into the population occurring through breeding, without significant input via immigration. The primary consideration for selecting the panhandle region for this study was the fact that 99 % of crocodile nesting and recruitment occurs in this region (Graham *et al.*, 1992). This study was undertaken to investigate the population status and ecology of the panhandle Nile crocodiles (Figure 4) to contribute to their management and conservation. Chapter 1 of this dissertation provides a review of literature of crocodilian ecology and the methodologies currently employed in crocodilian research. The

population status, including the abundance and survival rates of individual size classes were estimated in Chapter 2, using capture-mark-recapture methods. Following the determination of abundance, nocturnal spotlight and aerial survey methods were critically evaluated for their usefulness in the monitoring of the panhandle crocodile population (Chapter 3). Chapter 4 assessed the current breeding status and patterns of the population through nesting surveys. The morphometrics and growth rates were then investigated for the panhandle population and compared with several other African Nile crocodile populations (Chapter 5). The penultimate chapter (Chapter 6) reported the movement patterns of the panhandle crocodiles from the capture-mark-recapture data. Chapter 7 concluded this PhD dissertation with the production of a management plan for the conservation and sustainable use of the panhandle crocodile population, to be submitted to the Department of Wildlife and National Parks, Botswana.

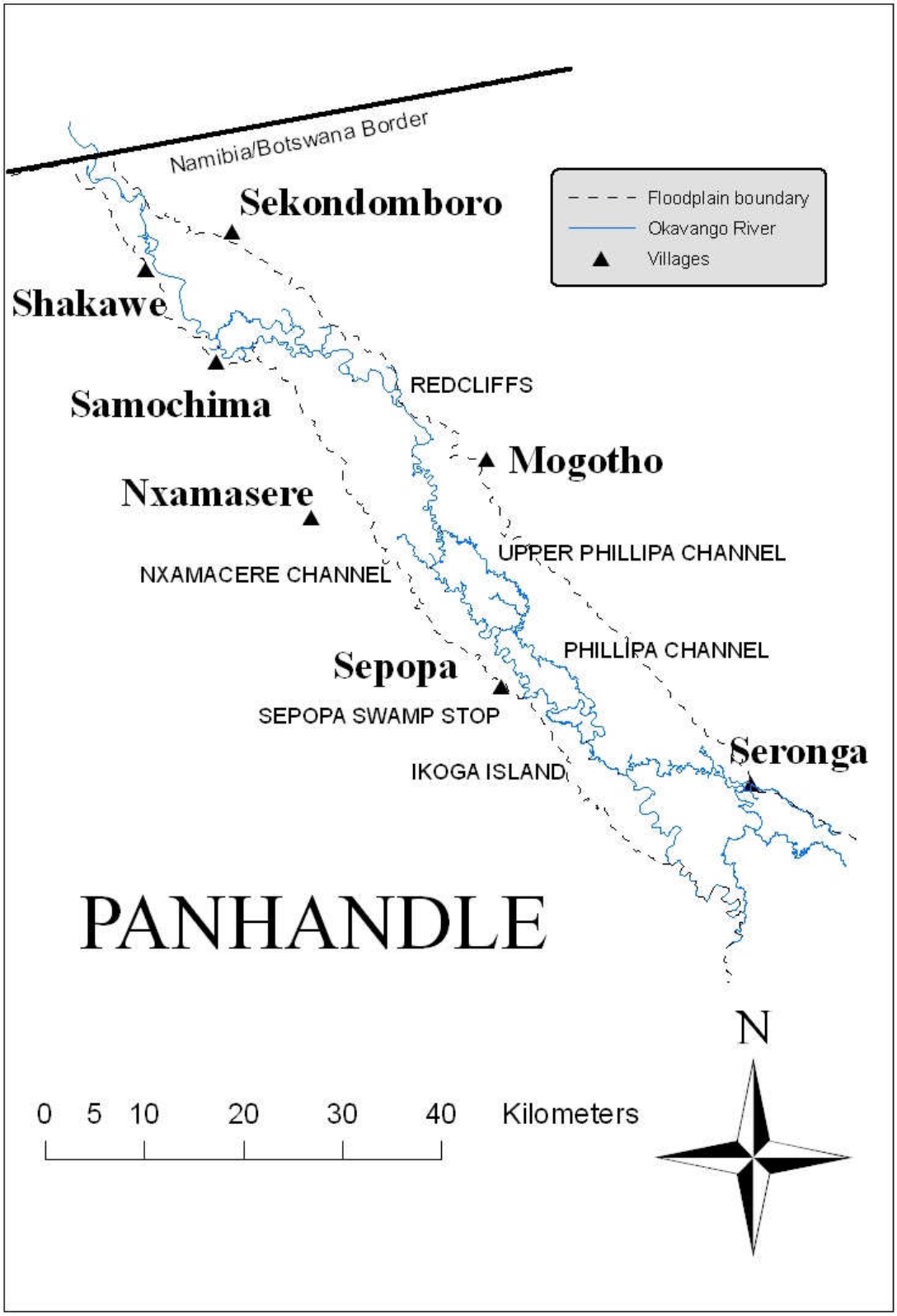

Figure 4. The panhandle region of the Okavango Delta, including 303 km of permanent, accessible channels, in which 99 % of the recruitment, through breeding, occurs.

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CHAPTER 2:

ESTIMATING THE SIZE, STRUCTURE AND SELECTED POPULATION DYNAMICS OF THE NILE CROCODILE POPULATION (2002 - 2006) IN THE PANHANDLE REGION OF THE OKAVANGO DELTA, BOTSWANA, USING MARK-RECAPTURE TECHNIQUES.

2.1 ABSTRACT

The population status of the Nile crocodile in the panhandle region of the Okavango Delta, Botswana, was assessed using a combination of capture-mark-recapture surveys, spotlight surveys and aerial surveys. The Okavango Delta is a closed system, and recruitment into the wild population can only occur through successful breeding, of which 99 % takes place in the panhandle region. This population has undergone several periods of over-utilization, which has resulted in the reduction of recruitment through breeding and the decline of the population as a whole. A capture-mark-recapture experiment was conducted continuously from 2002 - 2006 to estimate the current crocodile population in the panhandle, and estimate survival and recapture parameters for the population. Surveys were conducted by motorized boat at night, and crocodiles were located using a spotlight. A total of 1717 individuals, ranging in size from 136 mm - 2780 mm SVL, were captured and marked using the scute-removal technique. Yearlings were most often caught and made up 59.3 % of the total captures and 75 % of recaptures, with the successful capture of 81 % of all yearlings encountered. Survival and recapture estimates confirmed a size-dependent increase in wariness and survival within the population. The number of yearlings was estimated using a Bayesian technique, and these estimates were extrapolated for the other size classes using size distribution data that included all animals encountered on the river over a two year period. The total annual population in the panhandle region of the Okavango Delta was estimated to be 2 570 ± 151.06 individuals, with an adult population of 649.2 individuals. The adult and sub-adult sex ratio was slightly female-biased, and the number of breeding females was estimated to be 364 individuals. It was concluded that this population cannot sustain the further harvest of breeding animals prior to the increase and stabilization of the population.

2.2 INTRODUCTION

Monitoring animal population dynamics through time is the key to discovering and understanding the ecological issues related to the success of animal populations (Gibbs, 2000). Capture-mark-recapture (CMR) was developed for field studies in which the count statistics are numbers of marked and unmarked animals caught or, in some circumstances, sighted. Their purpose was originally to estimate population size in mobile animals (Nichols, 1992; Petit & Valiere, 2005). The general principal of CMR experiments is to capture and individually and unambiguously mark animals in a first capture session and then to record the proportion of marked individuals in subsequent capture sessions (Otis *et al.*, 1978; Nichols, 1992; Williams *et al.*, 2001; Nichols *et al.*, 2004). In the simplest models, population size is then estimated from the proportion of marked to unmarked animals, assuming the random mixing of individuals between capture/recapture sessions, and the equal likelihood of subsequently capturing marked and unmarked animals (Nichols, 1992). Traditional CMR models provide ways of estimating encounter (or recapture) probabilities, population size and survival rates (Nichols, 1992). Mark-recapture based population estimates have been used extensively in crocodilian population studies (Chabreck, 1963, 1966; Bayliss, 1987; Hutton & Woolhouse, 1989; Ross, 1998; Kay, 2004b; Letnic & Connors, 2006; Combrink *et al.*, in Press), and remain the most effective and accurate way in which to estimate abundance.

These estimates are fundamental requirements for management of animal populations, for example, to identify areas where intervention may be required for effective management, such as harvesting strategies or conservation decisions. The 1980's saw a shift in emphasis away from estimating population size and CMR data were instead collected for the purpose of estimating population survival and recapture rates[4] (Lebreton *et al.*, 1992). This shift was advantageous because survival estimators were a great deal more robust to the partial failure of assumptions, than were estimators of population size (e.g. assumption of homogeneity of individuals to capture or recapture). When estimating survivorship, a random mixing of marked individuals is not necessary - this is only the case when estimating population size (Lebreton *et al.*, 1992).

The purpose of this study was to model survival and recapture rates of crocodiles in the panhandle region of the Okavango Delta, and to estimate population abundance using capture-mark-recapture techniques. This information is crucial when assessing the status of any animal

[4] In the past, survival was often estimated without recapture rate, but this was misleading as the probability of recapturing an animal is the product of the probability of survival and the probability of encountering (recapturing) the animal again.

population, and even more so when that species is utilized commercially and harvesting takes place from the wild population. In addition, this river system is regarded as a "closed" system (i.e. not open to immigration from other systems), and therefore this particular crocodile population has no possibility of being strengthened genetically by immigration from elsewhere. In this regard it is important to note that it is the effective population size (the number of animals actually contributing genetic material to the next generation) rather than the actual number of living individuals, that directly influences population viability (Bishop *et al.*, in Press). The loss of genetic variability within a population theoretically decreases the likelihood of that population being able to effectively deal with stochastic environmental processes and thereby persist through time (Frankham, 2002). Without efficient research, management and protection of the population, it is therefore possible that this "keystone species" will falter, with dramatic consequences to this sensitive and finely-balanced ecosystem.

2.3 MATERIALS AND METHODS

2.3.1 Study Site

The Okavango Delta is situated in the north-eastern region of the landlocked country of Botswana, in Southern Africa. Botswana is bordered by South Africa, Zambia, Zimbabwe and Namibia (Figure 5). The Delta itself is an alluvial fan, (Mendelsohn & el Obeid, 2004) that never reaches the sea. The northern part of the Delta, known as the panhandle region[5] (Figure 6) is characterized by a labyrinth of deep-water, permanent, fast flowing channels, lagoons, and annually inundated floodplains. Further south-east (downstream), a few main channels lined by tall reeds (primarily *Phragmites australis*), split away from the main channel and carry the remainder of the Okavango's water southwards through the fan, to eventually discharge into the Boteti River, depending on the size of the flood. *Cyperus spp.* (commonly known as Papyrus), which dominate in the panhandle region is replaced by other reeds (*Pychreus machrostachyus*), sedges and grasses (eg: *Miscanthidium junceum*) in the temporary swamp. Scattered throughout the southern portion of the fan are thousands of islands produced primarily by termites, but also by various other processes such as aggradation (McCarthy, 2004).

The research for this study was concentrated in the panhandle region, covering a total length of 303 km of permanent channels. As mentioned above, the Okavango system is a closed system where all recruitment into the population occurs through breeding, without significant input via

[5] The Okavango River enters north-eastern Botswana and forms a very broad, linear floodplain known as the panhandle, which eventually fans out after encountering the Gumare fault, to form the Okavango Delta, the alluvial fan (Mendelsohn & el Obeid, 2004).

immigration. By far the most important consideration in the selection of the panhandle region for this study was the fact that 99 % of crocodile nesting occurs in this region (Graham *et al.*, 1992).

2.3.2 STUDY ANIMAL

Crocodilians belong to the group of archosaurs which also included the extinct thecodonts, the dinosaurs, the pterosaurs (flying reptiles) and the ancestors of the birds (Gatesy *et al.*, 2003). Crocodilians of the most advanced kind, the Eusuchians, first appeared some 140 to 65 million years ago, and all extant crocodilians belong to this suborder. Crocodilians once comprised over 125 genera (Romer, 1956), but have been reduced to just eight in recent times. There are some 23 species (King & Burke, 1989) found throughout the world today, belonging to the Family Crocodylidae, which is further divided into 3 subfamilies: a) Crocodylinae, b) the Alligatorinae and c) the Gavialinae.

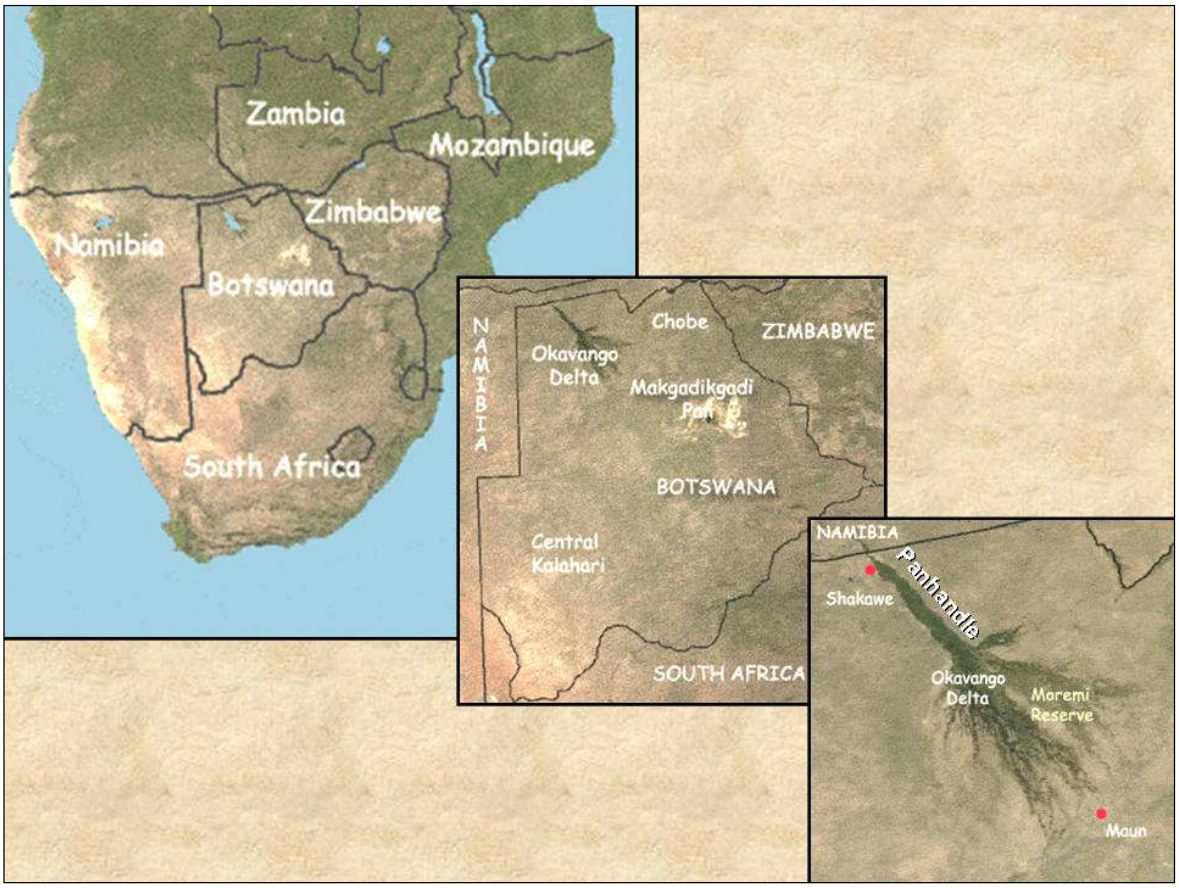

Figure 5: The study area of the Okavango Crocodile Research Group, in the panhandle region of the Okavango Delta, Botswana
(source: **http://www.egnu.com/maps/okavango_map.html**, accessed on 28/07/07).

Crocodilians exist throughout the tropics and are considered to be a “keystone” species (Craighead, 1968; Thorbjarnarson, 1992; Ross, 1998) that maintain ecosystem structure and function. A keystone species is a species that has a disproportionate effect on its environment relative to its abundance, and removal or decline of that species from the ecosystem will have a dramatic effect in maintaining ecosystem structure and function. In the case of crocodiles, this may include selective predation on fish species (Cott, 1961; Pooley, 1982b), recycling nutrients, and maintenance of wet refugia in droughts (Thorbjarnarson, 1992; Ross, 1998). Crocodilians are the largest predators in their aquatic environments, with terrestrial mammals including humans and livestock falling victim to them. Many species worldwide are exploited for their skins, and many populations are threatened due to hunting for trade (Glastra, 1983; Mourao *et al.*, 1996; Thorbjarnarson & Velasco, 1999; Thorbjarnarson *et al.*, 2000; Santiapillai & Silva, 2001). In addition to this, populations are threatened by habitat loss, pollution and over-harvesting (Thorbjarnarson, 1992).

The Nile crocodile is among the best known biologically of all crocodilian species and occurs in 42 African countries, of which only approximately 20 populations have been scientifically assessed, the results of which are outlined in Thorbjarnarson (1992) and Ross (1998). Crocodilians are long-lived animals with high mortality rates in the first year after hatching due to predation (Woodward *et al.*, 1987). Crocodilians exhibit indeterminate growth, and *adult male* Nile crocodiles can *attain* a length of 5 m, although adults average 2.8 – 3.5 m in length (Alexander & Marais, 2007). The species can tolerate a broad range of habitat types including small brackish streams, fast flowing rivers, swamps, dams and tidal lakes and estuaries (Pooley, 1969; Pooley, 1982b; Leslie, 1997). Crocodilians are ectothermic and regulate their body temperature behaviourally by moving between sun-exposed sandbanks and the water. They are oviparous and exhibit parental care throughout the incubation period and for a limited post-hatching time (Thorbjarnarson, 1992). Nile crocodiles lay eggs in a chamber which the female excavates for this purpose, depositing 40-80 eggs, which are then covered by sand in which they incubate for approximately 90 days (Leslie, 1997). Along with several other reptile species, crocodiles exhibit temperature-dependent sex determination (Brazaitis, 1969; Hutton, 1987; Crews, 1994; Leslie, 1997; Boussarie, 1999; Deeming, 2004). The sex of the hatchlings is determined by the average incubation temperature in the middle trimester of the incubation period. In other words, sex chromosomes are absent. Eggs are routinely predated by many species, including a primary predator, the Water monitor, *Varanus niloticus* (Trutnau & Sommerland, 2006), which may be responsible for the predation of up to 50 % of nests. In Australia, approximately 25 % of *C. porosus* clutches usually hatch in the wild due to predation and flooding (Webb & Manolis, 1993).

The global population of the Nile crocodile is listed as "Least concern" in the 2004 IUCN Red list (IUCN, 2004). This list includes taxa that do not qualify (and are not close to qualifying) as threatened or near threatened. However, populations may be rare or threatened in some parts of the species' range through over-exploitation and habitat destruction. The earliest written records on *C. niloticus* in a text entitled "The History of Herodotus", written by Herodotus in 440 B.C.E., and writings on the crocodile also appear in 58 BC (Guggisberg, 1972). Cott (1961) mentions commercial hunting of Nile crocodiles as early as the 1930's, after which widespread eradication programs were implemented, extending into the 1950's and 1960's (Cott, 1961; Parker & Watson, 1970; Leslie, 1997). Widespread and largely uncontrolled hunting for commercial trade of crocodiles abated with the intervention of international legislation by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), which lists the Nile crocodile in Botswana on Appendix II (CITES, 2007).

A species-level management strategy by the Crocodile Specialist Group, which is part of the IUCN's Species Survival Commission, (Thorbjarnarson, 1992) has also lead directly to the reduction of persecution of this species. The largest current threats to the Nile crocodile is conflict with people (Ross, 1998; Combrink *et al.*, in Press), hunting (Cott, 1961; Abercrombie, 1978) and habitat loss and pollution associated with increasing human population densities (Cott, 1961; Pooley, 1982a; Thorbjarnarson, 1992; Swanepoel, 1996). Human-crocodile conflict increases together with the frequency of encounter (Combrink, 2004; Thomas, 2006) and this conflict invariably results in the reduction of the wild population.

The Nile crocodile population in the Okavango Delta has undergone three periods of human-induced decline over the last century. In 1957, the Department of Wildlife and National Parks (DWNP) allowed a quota of 2 000 animals per year to each of two concessionaries. Between 1957 and 1969 an estimated 50 000 crocodiles were shot and trapped by hide-hunters (Pooley, 1982a). Taylor (1973) speculated that as many as 80 000 crocodiles could have been destroyed in the Okavango Delta during this cropping[6] period (Taylor, 1973). He was informed that 40 000 skins were marketed, and remarked that possibly only 50 % of animals shot were recovered. His considered opinion was that a total harvest figure of 50 000 animals was conservative.

[6] "Cropping" is defined here as the direct harvesting of animals from the wild for commercial use. Thorbjarnarson, J.B. (1992). *Crocodiles: An Action Plan for Their Conservation.* IUCN-The World Conservation Union, Gland, Switzerland.

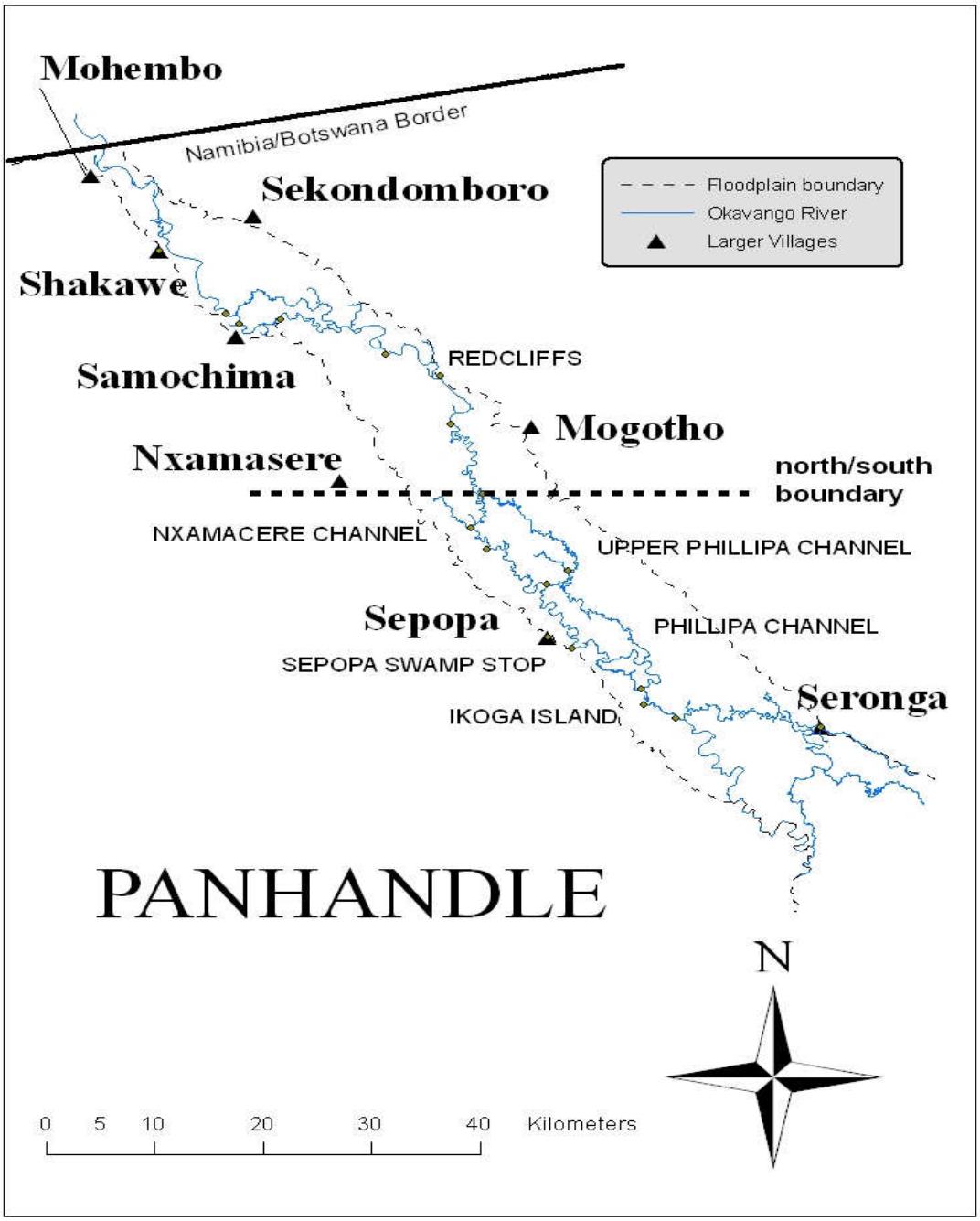

Figure 6. The panhandle region of the Okavango Delta, Botswana, showing the delineation (dotted line) between the "northern" and "southern" research areas. The data were divided into "northern" and "southern" populations, with the dividing line on the entrance to the Upper Phillipa channel. This was done to take into account the possible effects of a greater human impact on the northern population, where human densities were higher and therefore greater disturbance and disruption to the size class distribution was expected (Mendelsohn & el Obeid, 2004; Shacks, 2006). In addition, due to logistical practicalities, there was lower sampling effort in the northern panhandle.

In 1964 organized hunting ceased, and in 1974 all DWNP records pertaining to crocodile hunting disappeared, so actual harvest figures remain unknown. In 1973 the DWNP set a quota of 500 animals per year for the Botswana Game Industries (BGI) to resume hide hunting (Graham *et al.*, 1992). A report generated by Taylor (1973) testified to the fact that there was no population census carried out prior to the cropping operation, and the quota was determined "arbitrarily after due consideration by Game Department personal." The quota of 500 animals was filled in 1973, but only 440 crocodiles were shot in 1974 and the venture was hereafter regarded as uneconomic and disbanded. After a decade of no exploitation, crocodile farmers and ranchers removed 1053 live adults and 14 000 eggs from the system between 1983 and 1988 for commercial use in commercial operations. An aerial survey in 1987 estimated the crocodile population to be approximately 10 000 animals (Simbotwe & Matlhare, 1987a). Additionally, a further nine adult crocodiles (three males and six females) and approximately 2000 eggs were collected annually in August / September from 2003 - 2007 in this region for the stocking of the Krokavango crocodile farm in Samochima, near Shakawe. This was undertaken without the benefit of any scientific validation prior to the issuing of permits by the DWNP.

Crocodiles' life histories are categorized by slow development, long life and delayed and repeated reproduction, where the risk of reproductive failure is minimized by repeated breeding rather than by maximizing output (Tucker, 1995). Vital statistics (survivorship, fecundity, growth rates and age [size-class] structure) must be quantified for the sound management of commercially exploited species, or the impacts of management strategies cannot be predicted (Kay, 2004a, b). Although *C. niloticus* has been commercially exploited in the Okavango Delta for the past five decades, the demographic parameters and hence effects of harvesting of this population remains unknown. Therefore, this study was undertaken to determine the current population status and demographic trends of the Nile crocodile in the panhandle region of the Okavango Delta.

2.4 MATERIALS AND METHODS

2.4.1 Capture-mark-recapture

The CMR program was initiated in the panhandle region of the Okavango Delta in January 2002 and continued until December 2006. Nocturnal surveys (night shifts) were undertaken using a 5.8 m flat-bottomed aluminium boat, fitted with a 60 hp Yamaha outboard motor, and crocodiles were located and approached using a 12 volt, 500 000 candle-power spotlight (Bayliss *et al.*, 1986; Hutton & Woolhouse, 1989; Walsh, 1989; Woodward & Moore, 1993; Da Silveira *et al.*, 1997; Platt & Thorbjarnarson, 2000; Thorbjarnarson *et al.*, 2000; Brown *et al.*, 2004). Due to a reflective layer in the eye, the tapetum lucidum (Grenard, 1991), crocodilian eyes reflect any bright light shone into them and exposed crocodiles can be located for distances in excess of 100 m, depending on a number of factors such as vegetation density, the strength of the spotlight and the relative position of the crocodile (Chabreck, 1966; Woodward & Marion, 1978; Hutton & Woolhouse, 1989; Combrink, 2004). Combrink (2004) provided a detailed literature review and description of the spotlight survey method.

In an attempt to collect data so that traditional capture-mark-recapture analyses could be conducted from discrete recapture sessions, four blocks of time were set aside in which the entire panhandle was surveyed from the Namibia / Botswana border near Shakawe village, to Seronga village (Figure 6), where the panhandle spreads into the Delta proper. These surveys were conducted in February 2005 and 2006 (flood - season), and August 2005 and October 2006 (low - water season). Unfortunately, the number of recaptures obtained in these four recapture sessions was not sufficient to estimate population size reliably and so these data were incorporated into the larger, ongoing capture-mark-recapture data set.

Nocturnal spotlight and capture surveys were conducted between 20h00 and 04h00 along pre-determined, non-overlapping transects. A team of four to six boat crew members were used, including one trained observer with at least one years' intensive spotlighting experience at the front of the boat. The boat was steered along the middle of the river at an average speed of 8 - 10 $km.hr^{-1}$ with the spotlight beam traversing an arc of 180^{0}, illuminating river banks, the water-vegetation ecotone, and the main river channel surface. Observers were changed at 30 minute intervals to avoid fatigue. When an eye shine (i.e. a crocodile) was observed, crocodiles were approached slowly and quietly and captured when possible, using the size-dependent techniques described below. Water and air temperature were recorded at intervals throughout each survey

period with a BATT-12 thermocouple meter (Physi-temp, CA, USA), when a crocodile was captured.

1. Crocodiles up to 1000 mm in length were captured by hand by gripping them around the neck and immediately bringing them on board, where they were secured by taping the jaws closed using a strong adhesive tape.
2. Crocodiles from 1000 - 2500 mm were noosed using an aluminium pole with a locking cable noose. The noose was placed over the snout and pulled tight around the neck. The animals were pulled on board the boat and physically restrained and secured.
3. Crocodiles from 2500 - 3500 mm, were noosed using a self-locking cable noose, fitted to a 3500 mm detachable pole and fastened to 25 m of climbing rope. The noose was positioned and pulled tight around the neck. These larger animals were allowed to tire themselves out before being secured and pulled on board. Animals over 3300 mm were processed on a nearby sandbank.
4. Animals larger than 3500 mm were captured using either box-traps or modified Pitman traps (see Leslie, 1997), set and baited on the river bank. These animals were noosed while in the trap or Pitman cable, and released on the rope to tire them out, before being pulled to the nearest safe river bank, where they were physically restrained and processed.

Animals were sampled with replacement (Underhill, 1990). Each animal was individually, unambiguously and permanently marked by scute[7] clipping (
Figure 7). Scutes corresponding to the number assigned to the individual crocodile were removed using a surgical scalpel (Jennings *et al.*, 1991; Leslie, 1997; Sutherland, 2006). Crocodiles over 1 400 mm total length were fitted with a bright colour coded and numbered plastic cattle ear tag on the most anterior single scute of the tail. These tags last for 2-4 years in the field. The animals were sexed and blood and urine samples were taken for later analysis (part of another study), after which various morphometric measurements were recorded. The crocodiles were assigned to classes based on snout-vent length (SVL), as the tails were damaged in many cases. The size classes[8] were: hatchlings < 169 mm, yearlings 169 - 389 mm, juveniles 390 - 663 mm, subadults 664 - 1158 mm, adults >1158 mm, following those of Leslie (1997).

[7] The scutes here refer to the raised scales on the tail of crocodile and are removed in a coded sequence to permanently and uniquely identify the individual (Figure 7).

[8] For the purposes of this study, "hatchlings" refers to crocodiles less than 170 mm SVL. Hatchlings are found in the system directly after the nesting season, usually from February to March, after which they enter the "yearling" phase. The "yearling" size class spans up to four years, while the crocodiles grow in SVL from 170 mm – 389 mm. During this stage of their growth, crocodiles are functionally and ecologically very similar. At approximately 390 mm SVL, they undergo a morphological (skull) and dietary shift and enter the "juvenile" size-class. The growth rates of young crocodiles are highly variable, and so these animals are classed in terms of size and ecological distinctiveness, rather than age.

This was necessary as it has been demonstrated that crocodiles of different sizes exhibit ecological and behavioural separation (Hutton, 1984; Games, 1990). When an animal was recaptured, its individual identity number was recorded and it was processed in an identical manner to calculate growth rates and movement patterns. Animals that were captured less than a week after being captured initially were not re-measured.

2.4.2 Assessing size class distribution

From June 2004 - October 2006, all crocodiles encountered on the river during the nocturnal capture surveys (described above) were recorded, whether or not they were captured, to collect accurate data on the size class distribution of the crocodiles seen in the river. Using only size class data from captured animals would have resulted in a bias in the size class distribution

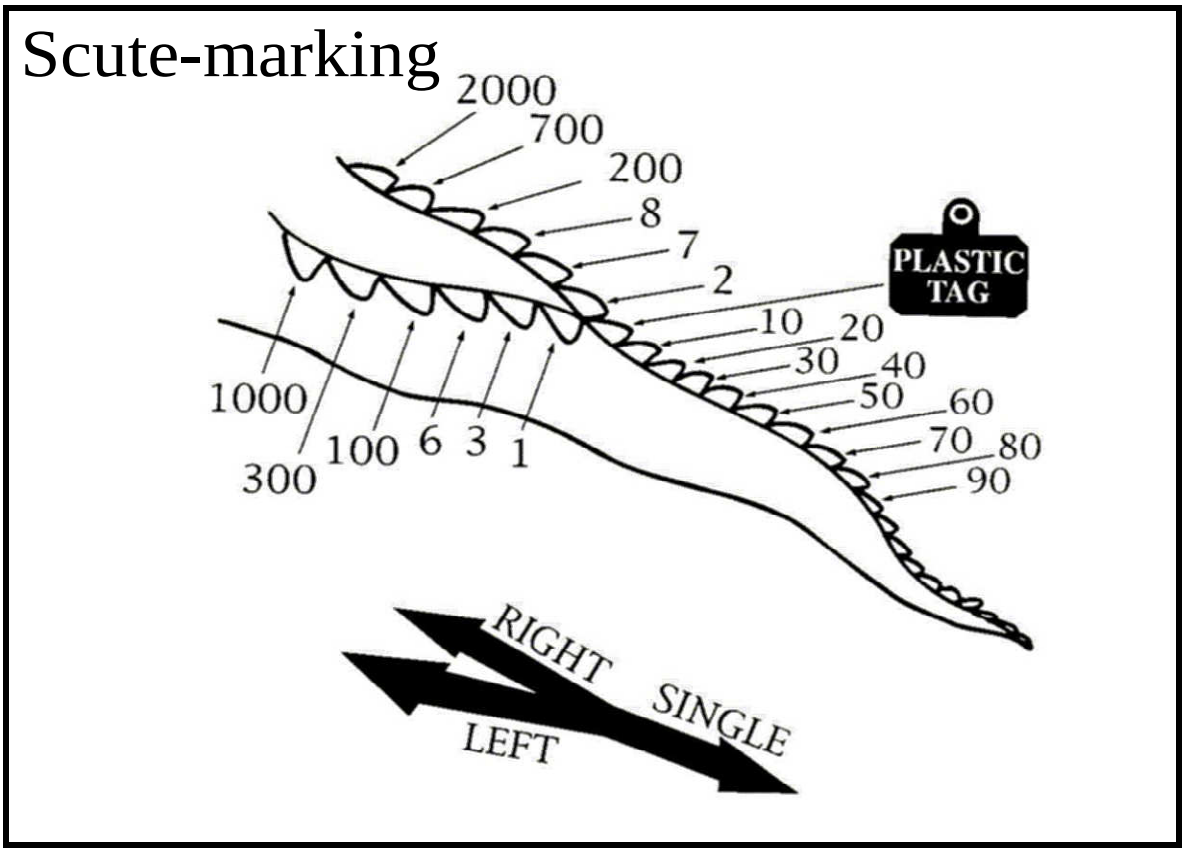

Figure 7. Diagrammatic illustration of the scute-removal method. Scutes corresponding or adding up to an individual crocodile's allocated number were removed with a sterile surgical scalpel (Leslie, 1997).

If, on the approach of the boat, crocodiles submerged, or were too large to handle from the boat (3.3 m and larger), the total length of the animal was estimated and its size-class determined.

When crocodiles submerged before the observers were close enough to reliably estimate size, they were recorded as “eyes only”. Each crocodile’s locality was recorded using a Magellan 301 S global positioning system (GPS), plotted on a satellite image of the delta, using ArcGIS v. 9 (ESRI, 2006). Captured crocodiles were released at the capture site after being processed.

2.4.3 Sexing of crocodiles

Animals were sexed by visual inspection of the cliteropenis (Webb *et al.*, 1984; Hutton, 1987). Subadult and adult crocodiles were used for the calculation of the sex-ratio of breeding animals, as these were the animals that were breeding or were imminent breeders. It was assumed that juveniles and smaller crocodiles had higher mortality rates (Pooley, 1982b; Webb & Manolis, 1993) and so these size classes were not included in the calculation of the breeding sex-ratios.

2.4.4 Data analysis

The data collected upstream and downstream of the upper entrance to the Upper Phillipa (Figure 6) were separated for analysis into the northern and southern panhandle regions. The crocodiles in the upper panhandle region were exposed to higher levels of human-induced disturbance than in the southern region (Shacks, 2006) and as early as 1973 there was a natural separation, defined by a paucity of crocodiles from Redcliffs (Figure 6) that ran a distance of approximately 8 km downstream (Taylor, 1973). It was assumed that this influence would have resulted in the animals in the northern panhandle being more wary of people, and thus violating the assumptions of the CMR models by altering capture probabilities between the northern and southern panhandle regions.

I. Survival and recapture estimates

The software program MARK version 3.2, (White & Burnham, 1999) was used to determine the most parsimonious Cormack-Jolly-Seber (Cormack, 1964; Jolly, 1965; Seber, 1965) model to fit the capture-mark-recapture data. This open population model was used because of the extended duration of the project, and subsequently allowed all data to be analysed simultaneously, using size as the individual covariate. Animals were therefore divided by size-class rather than age-class[9]. Each selected model’s survival and recapture parameters were estimated using maximum

[9] Age can only be determined if the animal concerned is captured as a hatchling and recaptured subsequently, and behaviour in crocodiles is determined by size rather than age. It is well documented, and easily observed in the field, that larger crocodiles are more wary of being approached and therefore capture probability is heterogeneous between cohorts (see e.g. Webb, G.J.W. & Smith, A.M.A. (1987). Life History Parameters, Population Dynamics and the Management of Crocodilians. In: *Wildlife Management: Crocodiles and Alligators* (eds G.J.W. Webb, S.C. Manolis & P.J. Whitehead). Surrey Beatty and Sons, Pty Ltd, Australia.).

likelihood approaches (Cooch & White, 2005) and models were evaluated using likelihood-based approaches. Models were ranked based on Akaike's information criterion (AIC) which reaches a compromise between the precision and model fit (Akaike, 1973). As the number of parameters increase (parsimony decreases), model fit improves, but the precision of the estimates of the individual parameters declines (Cooch & White, 2005). AIC ranking was also used to test for sources of variation in the selected models. Where models were nested, likelihood ratio tests (LRT) were used to compare models (Cooch & White, 2005). Data were not sufficient to stratify according to size-class in a multi-state[10] model. While this approach yielded results, data for all cohorts, with the exception of the yearling cohort, were too sparse to yield reliable estimates of survival and recapture probability and so these parameters were constrained to be linear functions of body length[11]. All snout-vent length (SVL) measurements were Z-transformed (i.e. covariates transformed to range from 0 - 1) and, with the logit link function, logit (survival) and logit (recapture probability) were calculated according to the equation below:

$$\log it(S) = \beta_o + \beta_1\left(\frac{x_1 - \overline{x_1}}{SD_1}\right)$$

Where β_o was the intercept and β_1 the slope of the estimated parameter i.e. survival probability (*Phi*; ϕ); or probability of recapture (*p*), x_i and $\overline{x_1}$ were the snout-vent length and mean snout-vent length, and SD_1 the standard deviation of this covariate.

True survival and recapture probability values were then calculated by back-transforming (Cooch & White, 2005; Williams *et al.*, 2001) according to the equation below:

$$p_i = \frac{e^{\beta o + \beta 1 xi}}{1 + e^{\beta o + \beta 1 xi}}$$

Where β_o and β_1 were the intercept and slope of the survival and recapture probabilities and *Xi and* $\overline{x_i}$ were the standardized value of the individual (Pollock *et al.*, 1984).

[10] The multi-state approach analyzes each cohort individually, calculating probabilities of survival, recapture and movement between cohorts.

[11] SVL is used as the continuous covariate "size" representative – total length can be misleading as often crocodiles' tails are damaged by predators.

II. Population estimates

The recapture data collected in the structured recapture sessions were too sparse to estimate population size using open population models within MARK. A Bayesian approach (Underhill & Fraser, 1989; Underhill, 1990) was therefore used to estimate the annual population size of yearlings in the panhandle. Hatchlings were excluded due to expected high mortality rates and low capture rates. Yearlings had the highest recapture rates, and population estimates were obtained for this cohort. As the recapture rates in the larger size classes were too low to obtain reliable abundance estimates for them, they too were excluded from the analysis. To obtain estimates for the larger size classes, the number of animals in the larger size classes was extrapolated based on size-class distribution data obtained from recording the size and location of all animals encountered between 2004 and 2006. These data were obtained during the night-shifts, and included all encounters, regardless of whether animals were captured or not, on the panhandle in 188 night shifts including 2 679 observations. Thus, seasonal variation was taken into account.

Demographic closure was assumed (Kay, 2004b) as yearlings did not move significant distances (Chapter 7) and in only one instance was a crocodile recaptured having crossed the natural historical north-south panhandle divide.

The assumptions that underlie this method (Du Feu *et al.*, 1983; Gazey & Stanley, 1986; Zucchini & Channing, 1986) were namely that: 1) the population was closed, so that there was no mortality, natality, emigration or immigration during the sampling period; 2) all individuals had the same probability of being captured, regardless of whether they were marked or not; 3) the captured individuals were all marked and released immediately. Also, the marking method had to be unambiguous and last for the duration of the sampling session.

The technique of estimating the number of yearlings follows:

Let N_{max} be a guess at the maximum possible number of crocodiles in the area. Let $p_i(N)$ be our estimate that the population was of size N after the ith crocodile has been handled. Initially, we set

$$p_0(n) = \frac{1}{N \max}, n = 1...N \max$$

Suppose that, when the *i*th crocodile was captured, the number of crocodiles already marked was *m*. Given that the population size was *N*, the probabilities that this crocodile is marked or unmarked were $\frac{m}{N}$ and $\frac{N-m}{N}$, respectively. If the *i*th crocodile was unmarked, it follows from Bayes' theorem that:

$$p_i(N) = k\frac{N-m}{N}p_{i-1}(N)$$

where:

$$k = \left(\sum_{N=m}^{N\max}\frac{N-m}{N}p_{i-1}(N)\right)^{-1}$$

Similarly, if the *i*th crocodile was marked:

$$p_i(N) = k\left(\frac{m}{N}\right)p_{i-1}(N)$$

where:

$$k = \left(\sum_{N=m}^{N\max}\frac{m}{N}p_{i-1}(N)\right)^{-1}$$

In this way, the probability distribution of the population size was iteratively refined for each year. Useful estimates of population size were given by the mean each probability distribution and 95 % confidence intervals were obtained from the 2.5 % and 97.5 % percentiles. Each unmarked crocodile that was captured shifted the distribution to the right, increasing the estimated population size. Similarly, each marked crocodile shifted the distribution to the left, decreasing the estimated population size. As the number of crocodiles processed, (*i*), increased, and provided the assumptions were met, the probability distribution became more concentrated, and the successive estimates of population size were more stable.

2.5 RESULTS

2.5.1 General

A total of 1717 individual crocodiles were captured from January 2002 to December 2006, of which 27 animals were trapped. These crocodiles ranged in size from 346 – 2560 mm SVL. Overall, 148 (8.6 %) hatchlings, 1018 (59.3 %) yearlings, 311 (18.1 %) juveniles, 177 (10.3 %) subadults and 63 (3.7 %) adults were captured. A number of individuals were recaptured more than once: 224 crocodiles were recaptured at least once, 44 at least twice, 7 at least three times and one was recaptured five times. Of all the yearlings that were encountered on the river, 81.0 % were successfully captured and a total of 75.0 % of recaptures were yearlings (Figure 8). Populations were estimated only for those years in which the proportion of recaptures was at least 10.0 %. Below this recapture rate, population estimates became inaccurate, with unacceptably high 95 % confidence intervals. While periodic surveys were conducted in the northern panhandle throughout the duration of the project, logistical constraints made it difficult to work in this area once the research team were based in the southern panhandle after 2002. Nonetheless, recapture sessions conducted in the northern panhandle after 2002 revealed very low capture and recapture rates, and only allowed for the estimation of population size during 2002.

2.5.2 Model selection and testing:

Models follow the notation in (Lebreton *et al.*, 1992). There were no gender specific differences in survival or recapture rates for yearlings (see also Kay 2004b), and so males and females were combined for the analyses. The most parsimonious model, according to the AICc values (the corrected or adjusted AIC value for each model) was the model Phi(SVL)p(SVL), where both survival (phi) and recapture parameters (p) were constrained by SVL as a covariate (Table 1).

The models making up the selected suite were subjected to a likelihood ratio test (LRT) to test for significant differences between them. As can be seen from the results of the LRT (Table 2), the model in which both survival and recapture probability were constrained [Phi(SVL)p(SVL], or where either parameter was constrained [Phi(SVL)p(.); Phi(.)p(SVL)] were significantly different from other less constrained models, suggesting that the AICc ranking of this model was valid.

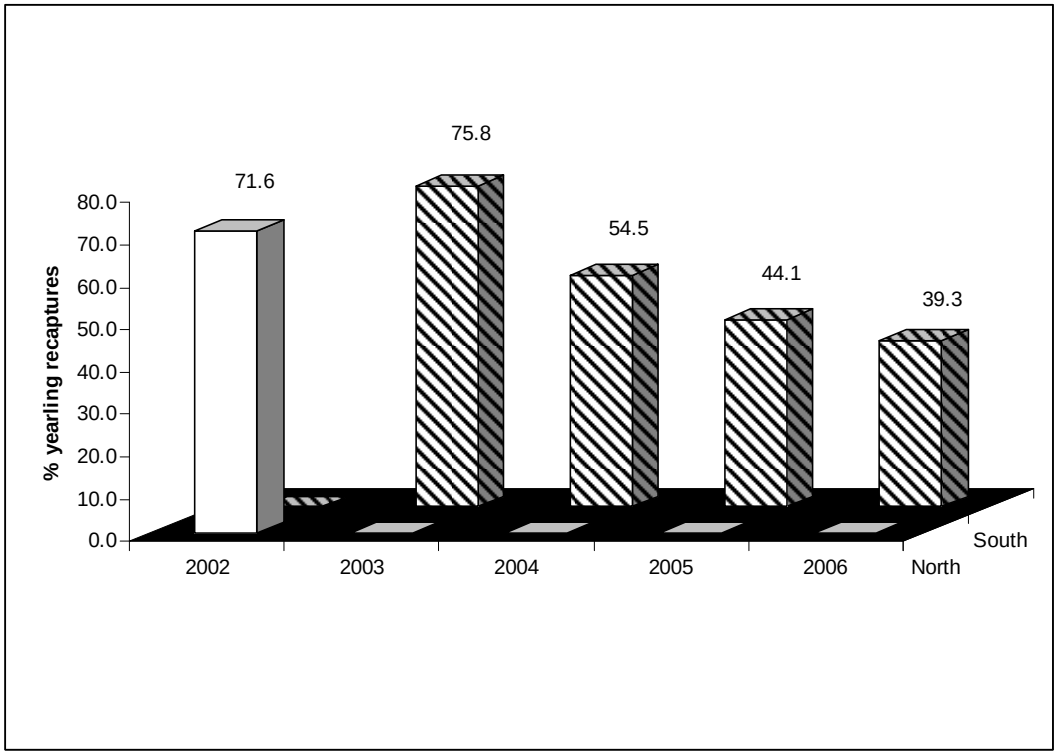

Figure 8. The proportion of yearlings making up recaptures from 2002 - 2006 in the panhandle. Annual yearling population estimates were only feasible where annual yearling recaptures made up over 10 % of captures. The figures above columns represent the percentage of total annual recaptures made up of yearlings. Striped columns represent the southern panhandle data, while clear columns represent the northern panhandle data.

Table 1. The selected models ranked according to Akaike's information criterion (AIC), with the most parsimonious model, as ranked by the AICc (the corrected AIC), listed in order from most parsimonious to least parsimonious.

Cormack-Jolly-Seber Model	AICc	Delta AICc	AICc Weight	Model Likelihood	# Parameters	Deviance
Phi(SVL)p(SVL)	518.358	0	0.79002	1	4	510.314
Phi(SVL)p(.)	522.346	3.99	0.10752	0.1361	3	516.32
Phi(SVL)p(t)	523.286	4.93	0.06722	0.0851	5	513.22
Phi(.)p(.)	524.728	6.37	0.03268	0.0414	2	520.715
Phi(t)p(t)	529.827	11.47	0.00255	0.0032	6	517.736

Table 2. The Maximum-likelihood ratio test results for the selected models in this study. Those models in which survival or recapture probabilities were constrained by SVL (Phi(SVL)p(SVL)) were significantly different from those in which either of the survival or recapture rate parameters were constrained, and also from the unconstrained model.

Maximum-likelihood Ratio Tests				
Reduced Model	General Model	Chi-sq.	Degrees of freedom	Probability.
Phi(.)p(SVL)	Phi(SVL)p(SVL)	5.808	1	0.016*
Phi(SVL))p(.)	Phi(SVL)p(SVL)	6.006	1	0.0143*
Phi(.)p(.)	Phi(SVL)p(SVL)	10.401	2	0.0055*
Phi(.)p(SVL)	Phi(SVL)p(t)	2.902	2	0.2343
Phi(.)p(.)	Phi(.)p(SVL)	4.592	1	0.0321*
Phi(SVL)p(.)	Phi(SVL)p(t)	3.1	2	0.2123
Phi(.)p(.)	Phi(SVL))p(.)	4.395	1	0.0361*
Phi(.)p(.)	Phi(SVL)p(t)	7.495	3	0.0577
Phi(.)p(.)	Phi(t)p(t)	2.979	4	0.5613

* = significant at probability < 0.05.

2.5.3 Estimating survival and recapture probabilities

The expected trends of increasing wariness and survival with increasing size were confirmed using the Cormack-Jolly-Seber model (Figure 9). Both survival and recapture rates were significantly affected by the size of the crocodiles, with smaller animals experiencing higher mortalities and a higher probability of being recaptured. Although Figure 9 illustrates very heterogeneous survival rates for the smaller size classes, these figures are not absolute as can be seen by the fairly large range depicted by the 95 % confidence intervals reported in Table 3.

2.5.4 Population estimate

Estimates for population size were obtained separately for each year, and for the northern and southern yearling populations (Figure 10). Data were too sparse to estimate the northern panhandle yearling population from 2003 - 2006, and for the estimation of the southern yearling population during 2002. The annual average population estimate of yearlings for the southern section of the panhandle was 538.55 ± 146.13. The 2002 yearling population estimate for the northern panhandle was 304.5 (95 % CI = 251 - 373) individuals. The total number of yearlings

estimated at any given time for the entire panhandle was 857 individuals (Table 4). Note that this estimate is of the total number of yearlings, which may be up to four years of age, in the panhandle system. About 25 % of this estimate would therefore be the annual number of "new" yearlings.

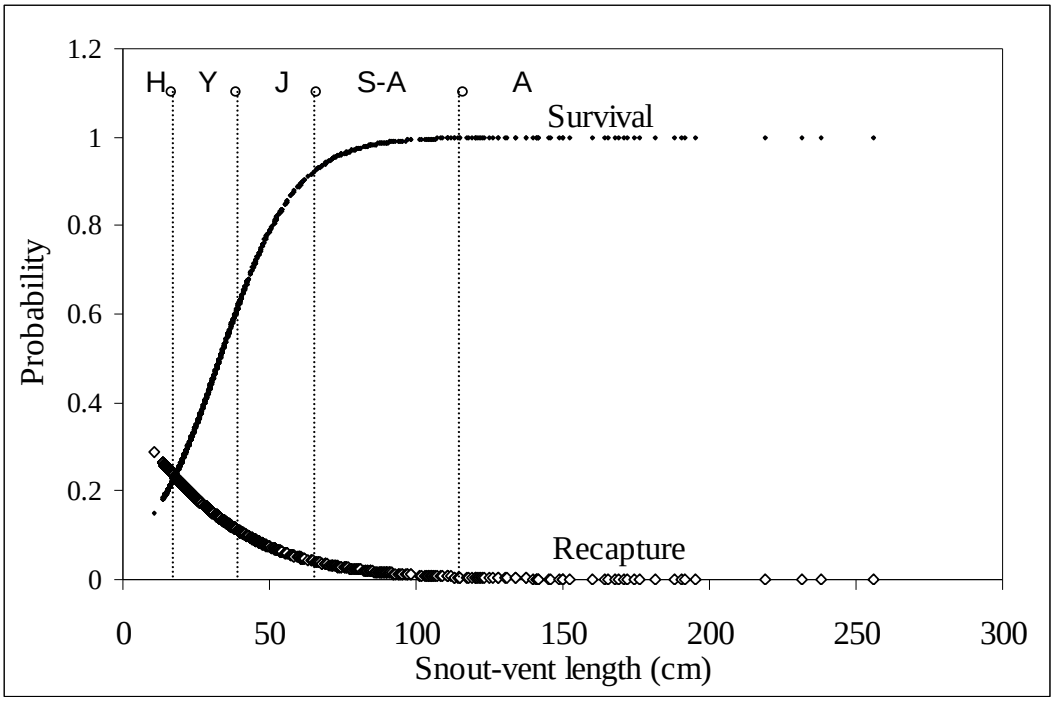

Figure 9. The survival and recapture trends for *C. niloticus* in the Okavango system, when both parameters were constrained by SVL.

Table 3. The logit survival and recapture probability estimates for Phi(SVL)p(SVL), where these parameters were constrained by SVL. To obtain the actual values illustrated in Figure 9, these values were transformed.

LOGIT Link Function Parameters of Phi(SVL)p(SVL)				
Parameter	Beta	SE	95 % CI	
			Lower	Upper
Phi Intercept	0.65	0.64	0.38	0.85
Phi slope	0.93	0.70	0.70	0.99
p Intercept	0.10	0.58	0.06	0.17
p slope	0.21	0.59	0.11	0.35

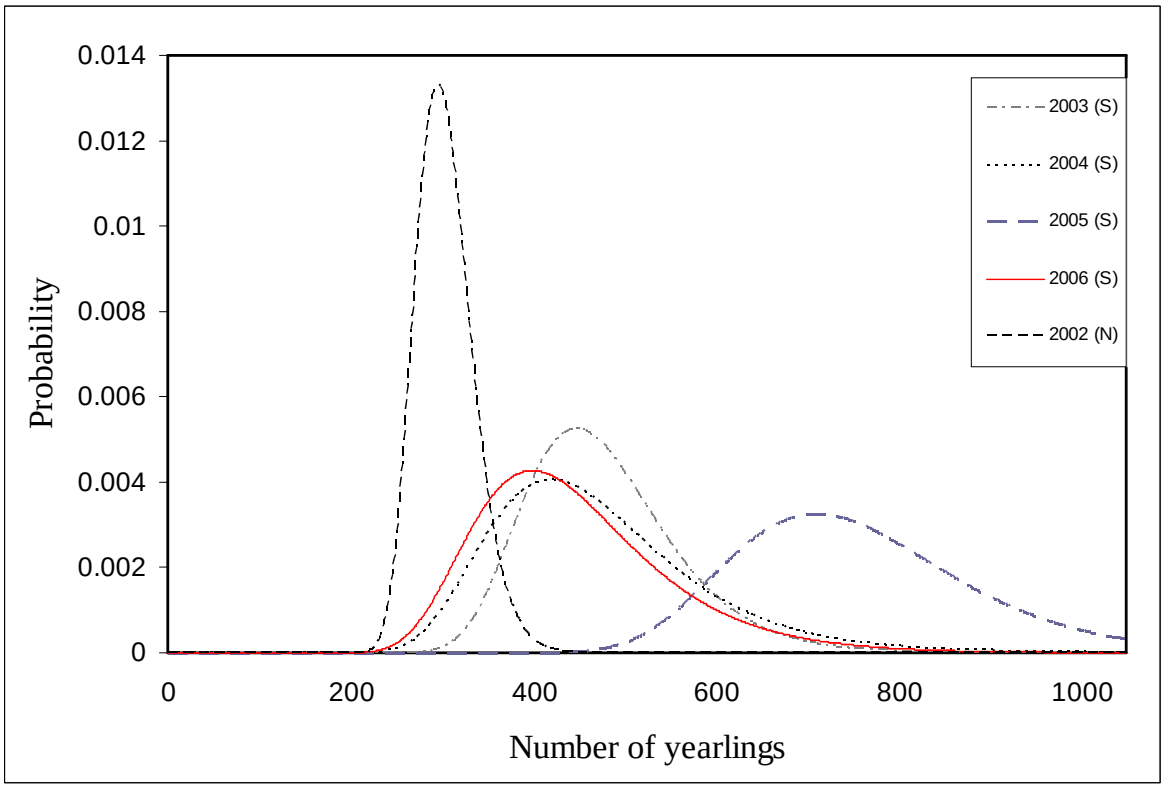

Figure 10. Maximum-likelihood probability distributions for the annual Bayesian population estimates of yearlings. The peak of each probability curve represents the estimate of yearling population for that particular year.

Extrapolating from the size class distribution data collected in 2004 (54 night shifts), 2005 (91 night shifts), and 2006 (43 night shifts), the total annual population in the panhandle region of the Okavango Delta was estimated to be 2 570 ± 151.06 individuals. Yearlings constituted one-third of the total population, while adult crocodiles made up 25 % of the population (Table 5). While many animals were not approached to distances close enough to get accurate size estimates, these were more likely to have been larger animals due to their increased wariness. However, in the absence of accurate size estimates, these animals were excluded from the analysis. The harmonic mean of the number of adults estimated for 2003 - 2006 was 649.2 individuals.

Table 4. Yearling population estimates calculated using the Bayesian method. Data were separated into northern and southern panhandle data sets as per Figure 6.

Region	Year	Recapture rate	Population estimate	95 % Confidence Interval	
				Lower limit	Upper limit
Southern panhandle	2002*		No estimate		
	2003	0.16	477.80	345	668
	2004	0.10	471.50	301	746
	2005	0.09	756.90	542	1063
	2006	0.05	448.0	287.0	709.0
Northern panhandle	2002	0.25	304.50	251	373
	2003**		No estimate		
	2004**		No estimate		
	2005**		No estimate		
	2006**		No estimate		

* no recaptures

** recapture data too sparse to estimate yearling population

Table 5. Size-class distribution based on all eye-shine encounters (spotlight observations) from 2004 - 2006, and population estimates for other cohorts from the extrapolation of these data for the whole panhandle. The population size class distribution in the panhandle was stable for each of the three years.

	Year	Hatchlings	Yearlings	Juveniles	Sub-adults	Adults
Size-class distribution (%)	2003*	0.90	33.35	21.17	19.23	25.35
	2004	0.75	29.00	22.50	21.75	26.00
	2005	1.65	40.38	17.71	15.58	24.68
	2006	0.29	30.68	23.30	20.35	25.37
Total estimated number per size-class	2003*	21	782	497	451	595
	2004	20	776	602	582	696
	2005	43	1061	466	410	649
	2006	8	806	613	535	667

* % occurrence was calculated as an average of 2004-2006

2.5.5 Sex ratio

The sex ratios obtained from all animals throughout the duration of the study revealed a male-bias for yearlings and juveniles (61.8 % and 61.2 % males respectively), followed by a female bias for the subadult and adult size classes (45.2 % and 44.7 % males respectively) (Figure 11).

The sex-ratio obtained from sub-adults and adults (combined) that were captured during night shifts and from trapping revealed that the ratio was female biased, with 44 % of subadults and adults in the panhandle male and 56 % female. The number of mature females in the panhandle, calculated from the sex-ratio, was 364 individuals.

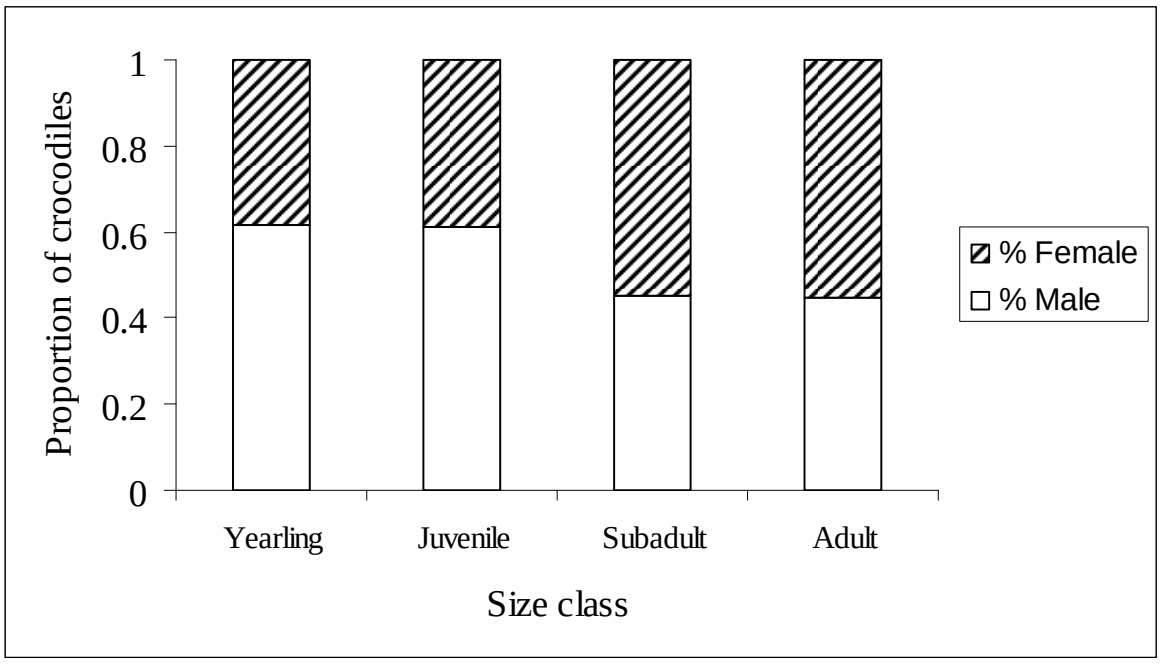

Figure 11. The sex ratio of each size class with the exception of hatchlings, for all crocodiles captured during the course of the study.

The proportion of animals within the smaller size classes (i.e. < 663 mm SVL) was higher in the panhandle when compared to some other regions in Africa (Table 6). The proportion of animals falling into the subadult and adult size classes was lower than the neighbouring Zimbabwe by more than 10 % (Table 6).

Table 6. Proportions of juvenile, subadult and adult size classes determined in various studies carried out in Africa.

Location	Juveniles	Sub-adults	Adults	Sum subadults and adults	Source
Okavango	55.4	19.2	25.4	44.6	This study
Kenya	50.0	31.0	19.0	50.0	(Graham, 1968)
Uganda	54.0	25.0	21.0	46.0	(Parker & Watson, 1970)
Zimbabwe	44.0	33.0	23.0	56.0	(Hutton & Woolhouse, 1989)
Mozambique	48.0	34.0	18.0	52.0	(Games, 1990)

2.6 DISCUSSION

2.6.1 Population estimate

Spotlight surveys have traditionally been used to assess and monitor populations by providing indices of population size and density (Bayliss *et al.*, 1986; Hutton & Woolhouse, 1989; Woodward & Moore, 1993; Ron *et al.*, 1998; Platt & Thorbjarnarson, 2000; Thorbjarnarson *et al.*, 2000; Brown *et al.*, 2004; Combrink, 2004). However, spotlight counts are inherently inaccurate because of visibility biases, and observers do not see all of the crocodiles present during a survey. Factors influencing the probability of detection of crocodiles include the type and structure of vegetation between the observer and the crocodile, river width, frequency of bends (sinuosity), position of the crocodile – submerged, on land etc, the orientation of the crocodile, and the wariness of the crocodile. Large animals tend to be more wary than smaller animals (Webb & Messel, 1979; Ron *et al.*, 1998). Over a substantial period of time, from June 2004 - October 2006, and including a total of 188 night-shifts, the spotlight counts of all encounters with crocodiles in the panhandle resulted in a reliable population structure and size-class distribution pattern. Mark-recapture experiments allow one to calculate correction factors for spotlight counts, in addition to population estimates (Chapter 4). Methods for estimating population abundance were conducted assuming a “closed” population (Williams *et al.*, 2001). However, it is very seldom that natural systems fulfil all the assumptions made by theoretical models. With crocodiles, different size classes differ in both life-histories and behaviour (Hutton, 1984). As such, the assumption of equal survivorship and recapture probability were violated to some degree (Figure 9) (Bayliss *et al.*, 1986). This violation was, however, minimized by selecting the yearling size class for application of the model. Kay (2004a) collected CMR data on Saltwater crocodiles in the King river (Australia) in 2001 and 2002. This data set was divided into hatchlings (< 1 year) and non-hatchlings (> 1 year) to reduce the problems associated with heterogeneity in capture and survival probabilities. Bayliss *et al.* (1986) found that recapture rates peaked between 900 mm TL (approximately 475 mm SVL) and 1200 mm TL (approximately 635 mm SVL), a range that corresponded to the yearling size class in this study.

In the case of the “no mortality” assumption, violation would lead to an over-estimation of the population if no more than 50 % of the captured crocodiles were recaptures. However, mortality had little effect on the estimates if marked and unmarked individuals had an equal probability of mortality, and this was assumed (Gibbons, 1968; Jennings *et al.*, 1991). The effects of mortality on the model (and thus the violation of the “equal survival” assumption of the Cormack - Jolly - Seber model) were minimized by dividing the data set into annual increments and further, into

the northern and southern panhandle region mentioned previously. Hutton and Woolhouse (1989) estimated crocodile population size using a modified Peterson estimate, using only those animals seen subsequent to the recapture session in the estimate. This had the advantage over other traditional mark-recapture estimates because mortality and loss of the marks uniquely identifying the individuals could be ignored. This was not feasible in the Okavango study as only using animals known to be alive at the time of recapture, would have restricted the data set to the point where population estimates would have been unrealistic. Violating the "equal catchability" assumption would be more problematic in terms of accurately estimating the population size of the panhandle crocodile population. If animals exhibited a "trap response" this would be difficult to quantify without recapturing many more animals for a third time (Underhill & Fraser, 1989), and so population estimates would not have been valid. Additionally, the larger size classes could not be used. Also, emigration and immigration (demographic closure) could not be assumed in sub-adult and hatchling animals as these are traditionally the size classes that disperse (Hutton, 1989). The fact that 81.0 % of all yearlings that we approached on the river were caught and 75.0 % of all recaptures were yearlings, illustrated their inexperience compared to the larger size classes with regards to being captured more than once. Bayliss *et al.* (1986) also demonstrated that the recapture rates of yearling *C. porosus* peaked in this size class, and rapidly declined as crocodiles grew larger.

There was no reason to believe that survivorship within the cohort varied between years. Even if the population was slightly over-estimated in this study as a result of mortality, the annual comparisons of population estimates would be comparable for population trends. With the removal of hatchlings from the northern panhandle (by crocodile farmers), estimates of the smaller size classes were likely to be over-estimates, as there was no recruitment of these animals. Estimates based on size-class distribution from the relatively undisturbed southern panhandle would still apply to the adult population as long as the adults remained undisturbed.

The proportion of animals making up the population showed some differences when compared to those from other regions of Africa (Graham, 1968; Parker & Watson, 1970; Hutton & Woolhouse, 1989; Games, 1990). While the proportion of juveniles (in this case, up to 663 mm SVL) was higher than those in other studies, they occur in low densities. The proportion of the adults and subadults, however, was lower than in other studies (Graham, 1968; Parker & Watson, 1970; Hutton & Woolhouse, 1989; Games, 1990). Had farmers not removed eggs from the wild, thereby reducing the number of smaller animals in the panhandle system, the proportion of subadults and adults would have been lower still (Table 6). Furthermore, if the population's recruitment, through breeding, had been healthy (Chapter 5) the numbers of

crocodiles in these size classes would have been more abundant, and the subadult and adult proportions would presumably have been significantly lower. Unfortunately, with eggs being removed by farmers, the number of hatchlings making up the population has been substantially reduced.

2.6.2 Sex ratio

Hutton (1987) found the Lake Ngezi crocodile population significantly skewed towards females. This included all size classes, and there was no evidence of mortality, dispersal or migration affecting the sex ratio. Mortality was restricted to animals < 120 cm TL and was not gender-specific. Dispersal and migration were negligible. The Okavango crocodile population had a higher proportion of sub-adult (45.2 % vs 37.0 %) and adult males (44.7 % vs 22.0 %) than the Ngezi population. The adult and subadult Nile crocodile population in St. Lucia (KwaZulu-Natal, South Africa) were again female-biased with only 38.1 % male animals (Leslie, 1997). The female-biased sex ratio was possibly due to gender-specific mortality from male-male competition in crocodilian populations. Hutton (1987) theorized that females would predominate amongst successful embryos, with the narrow temperature range in which males developed responsible for this bias. This ratio is therefore bound to fluctuate from year to year depending on environmental conditions. For example, the sex ratio in the King River (Australia) in 2001 revealed a sex ratio of 66.0 % male hatchlings and 76.0 % male non-hatchlings (Kay, 2004b).

With animals that exhibit temperature-dependent sex determination (TSD) and especially those such as Nile crocodiles that have a very narrow temperature range in which males are produced, global climate change can potentially have catastrophic effects on the hatchling survival rates, population sex ratios and thus population dynamics in general of a closed population such as that in the Okavango Delta. The incubation temperature of the clutch does not only affect gender. It also affects the probability that embryos will survive to hatching, growth rates before and after hatching, and the probability of hatchlings surviving to two years of age (Hutton, 1987; Webb & Cooper-Preston, 1989). The selective advantage of TSD is that it assigns maleness to embryos with high probabilities of surviving and good potential for post-hatching growth (Webb & Cooper-Preston, 1989). Males are produced from clutches in the Okavango panhandle when the average incubation temperature in the middle trimester is between 31.4 ^{0}C and 33.4 ^{0}C (Maciejewski, 2006). Although reptiles exhibiting TSD have previously survived global climate change (Nelson *et al.*, 2004), these changes have occurred over long periods of time and survival has been dependent on the species being able to track climate change to remain in tropical or sub-tropical environments. Over the past 100 years, global warming has increased by an unprecedented 0.6 ºC, and is projected to continue to rise at a rapid rate (Root *et al.*, 2003). In a

study of 143 species of animals, more than 80.0 % that showed changes were shifting in the direction expected on the basis of the known physiological constraints of the species (Root *et al.*, 2003). The rate of increase of global temperature far exceeds the ability of crocodiles to physiologically adapt to change, or to track these changes (Maciejewski, 2006). With regard to lethal limits for embryos in eggs, it is unlikely that they would be able to adapt physiologically, maintaining normal sex ratios over the long term. For example, if all nests increased to 35 ºC - 36 ºC, which means no nesting sites were possible in the 31 ºC - 33 ºC range, none would survive in those areas. In the way of speculation, the existing population may do well in the warmer conditions, even if they could not breed successfully, and could probably wait out 40 - 50 years without recruitment and still retain the capacity to rebuild populations if conditions returned to normal (Webb, Pers. comm., 2007). For a more detailed discussion on TSD and the potential effects of global climate change on crocodiles, see Maciejewski (1996)

2.6.3 The conservation genetics consequences of the overexploitation of the panhandle population

As mentioned above, small, isolated populations potentially face a much higher theoretical risk of drastic reduction or extinction through stochastic processes as they are not usually as buffered by allelic diversity or heterozygosity as a larger population would be against the effects of genetic drift or selection (Frankham, 2002). It is therefore necessary to monitor the levels of genetic diversity within a threatened population. The removal of eggs and adults from this already overexploited population, without any release back into the wild or immigration of new animals, has potentially dire consequences in this system. In a study investigating the effective population size of the panhandle population, it was found that moderate levels of heterozygosity had been maintained through the periods of exploitation, despite the specific targeting of adults (Bishop *et al.*, in Press). Bishop *et al.*, (in Press) suggested that the longevity and delayed sexual maturity of Nile crocodiles may have acted to buffer the expected effects of hide-hunting and the removal of breeders for farming purposes (i.e. reduced heterozygosity). However during this period, the effective population size (N_e) of the panhandle crocodiles has been reduced five-fold. Parental generation N_e has decreased from ~ 480 individuals to a current estimate of ~ 90 individuals (Bishop *et al.*, in Press). This result suggested an increased susceptibility for this population in terms of continuing decline as a function of genetic drift and selection, which results from low population size rather than a lack of heterozygosity (Bishop *et al.*, in Press). At the current effective population size, allelic diversity and heterozygosity will continue to decline through time due to the effects of genetic drift (Bishop *et al.*, in Press). The minimum N_e required to maintain sufficient genetic variation to allow a population to persist through stochastic events varies between species, depending on their life-histories (Bishop *et al.*, in

Press). It is generally accepted that maintaining > 90 % of allelic variation will ensure a populations persistence (Spielman *et al.*, 2004). Therefore, to maintain > 90 % of the current allelic diversity and heterogeneity over the next 100 years, it was suggested that an effective (stable) population of at least 150 animals would be required. This equates to a total population of 4200 animals, and an adult population of approximately 1060 individuals (Bishop *et al.*, in Press). At present the adult population averages 649 individuals.

2.6.4 The survivorship / recapture model

When using the most restrained model, Phi(.)p(.), all individuals are assumed to be the same, and there is no time variation in the model. This was clearly not the case. While it may have been feasible to fix time variation to a constant, we know that individual crocodiles differed in both survival and recapture probability (Webb & Smith, 1987). This difference was highly correlated to the size of the individual. As animals grow, the suite of natural predators utilizing crocodiles as a food resource diminishes, and the likelihood of survival increases, especially in the presence of unlimited food availability. In the Northern Territory of Australia, at least 25 % of *C. porosus* eggs usually hatch (Webb & Manolis, 1993); 54 % of hatchlings survive to one year; 30 % of one-year old crocodiles survive to two years; 60 % of two-year olds survive to three years of age; 56 % of three-year olds survive to four years of age; 56 % of four-year old crocodiles survive to five years (Webb & Manolis, 1993). Approximately 18 crocodiles in 1000 eggs laid therefore survive to five years of age, after which the mortality rate is unknown. Larger animals are also more wary of people, having learned that encounters with people are nearly always negative in the panhandle, as in other regions (Kay, 2004a), and larger animals are therefore less likely to be captured and are highly unlikely to be recaptured.

In addition to the large confidence intervals surrounding the slope for the survival parameter, it must be noted that this slope represents data collected over four years, and so the cumulative survival rate for the smaller size classes is low. Had there been enough recapture data to perform this analysis over a shorter time-period, for example one year, the survival rate would most probably have been more stable between yearlings. This has yet to be tested. There are many cases in the wildlife literature in which model assumptions are not stated or are misunderstood (Skalski *et al.*, 2005). One cannot simply apply a model without validating its assumptions and demonstrating a clear understanding of its meaning. When this is not done, no clear indication of the degree to which the model accurately represents the data can be obtained. In addition, future researchers cannot improve on methods of data collection or the accuracy of the model.

2.6.5 Human-induced disturbance

Disturbance caused by boat motors has a negative impact on nesting birds, mammals and reptiles that are reliant on the river for nesting sites and other resources (Mbaiwa, 2002). Mbaiwa (2002) noted that crowding of tourist facilities and noise pollution generated in these areas negatively impacted on the river-dependent fauna, and suggested that the Okavango Delta was likely to be environmentally degraded in the near future if measures were not taken to address the problem. Fishermen and reed-cutters destroy eggs and nests as they find them and female crocodiles are in general wary of people and often fail to protect their nests from human intruders. The papyrus beds are burned every year during the nesting season (Pers. obs., 2003-2006; Shacks, 2006) causing females to abandon nests which results in hatchlings becoming nest-bound due to the growth of vegetation over nesting cavities. It has been reported that only 60 % of mature Okavango females come into breeding condition annually (Detoeuf-Boulade, 2006) and only 14 % - 23 % of these females were nesting each year (Chapter 5). This figure suggests an outside influence such as those mentioned above, significantly lowering potential recruitment. The proportion of yearlings making up the total number of recaptures diminished predictably with time (Figure 8). This may very well have been a result of the removal of hatchlings from the northern panhandle region. The panhandle population, like the *C. niloticus* population studied by Cott (1961), and the *C. porosus* population studied by Webb & Messel (1978), is an exploited population. As such, there are few adult animals remaining (Cott, 1961; Webb & Messel, 1978). It is possible that the previous removal of breeding animals and minimised recruitment leading to the overall decrease in the number of animals in all size classes, the number of smaller animals coming through the system is also too low to maintain the current adult population in the near future.

2.6.6 Crocodile Ranching

The benefits of crocodile ranching are undisputed. In Australia, *C. porosus* have been protected since 1971 and the population of wild, non-hatchling crocodiles has increased by 50 % since farming was introduced in 1984. The population increased by 4-5 % per year during the 1980's and early 1990's (Webb & Manolis, 1992; Webb *et al*., 1994). With strict application and enforcement of legislation, the crocodile population and all those involved (includes community employment, improvement of local infrastructure, improved commercial and subsistence fishing, ecotourism opportunities etc) will benefit from crocodile ranching activities. It has been understood for some time that it is better to harvest eggs or smaller animals in stocking programs than to remove breeding animals from the wild, (Graham, 1968; Webb & Manolis, 1993) as

crocodiles in their first year generally suffer a high mortality anyway. Modelling virtual marine turtle[12] populations (Mazaris *et al.*, 2006) revealed that increasing the survival rate of the first year cohort contributed positively to overall population survival and reduced extinction probability to very low levels. Survival of the pelagic juvenile cohort (1-4 years) was the most critical parameter with regard to maintaining viable populations, and when a high range of pelagic juvenile mortality was used in the models, population extinction probability remained high, even if survival in the first cohort (0-1 years) was increased. If these trends hold true for crocodile populations, then ranchers aiming to release animals back into the wild should rear them into the juvenile phase, and so out of the high-mortality phase, before releasing them. However, rearing crocodiles in such close proximity can increase the spread of diseases at a much more rapid rate than would be experienced in the wild. Adult survival was the second most important parameter influencing turtle population survival (Mazaris *et al.*, 2006). Turtles are defenceless when on land and this would realistically only be a problem for crocodiles if cropping or farming activities removed breeding animals from the wild. In a study on American alligators, Temsiripong *et al.*, (2006) found that artificially incubated alligator hatchlings released outside of the maternal alligator's home range had lower recapture probabilities (and by implication, lower survival rates) than either naturally incubated hatchlings or artificially incubated hatchlings released near the original nest site. In addition to this, artificially incubated hatchlings were approximately 6 % shorter than naturally incubated hatchlings, approximately nine months after hatching. They concluded that repatriation of hatchlings probably would not have long-term effects on populations because of the resiliency of alligator populations to alterations of early age-class survival and growth rates. They further stated that repatriation of hatchlings may be an economical alternative to repatriation of older juveniles for population restoration. However, the location of release may affect subsequent survival and growth. These conclusions are interesting in that it is commonly believed that ranched crocodiles should be released after the initial “high mortality” phase, as juveniles (see Lang, 1987). This is, however, highly related to the density of crocodilians in the population under study, and should be assessed scientifically before moves are made to decrease the time that ranched animals remain in the ranches before repatriation. As Child (1987) reports, released Nile crocodiles in Zimbabwe (legislation requires a 5 % restocking rate at a total length of 1.2 m) have prospered, judging from mark-recapture results. However, the repatriation legislation has been very sparsely enforced in Zimbabwe.

[12] Marine turtles and crocodilians share many life-history parameters. Both are K-strategists and exhibit TSD and need a terrestrial environment for nesting. They exhibit high levels of mortality in the first year, and these rates decrease with age.

The effective management of crocodiles in the Okavango Delta, and indeed the whole of Botswana, affects all communities, at all levels. Only about one sixth of the land allocated to wildlife in Botswana has the ability to generate high economic value from wildlife utilization. This includes the land around the Okavango Delta, the northern riparian systems, and some pans (Barnes, 2001). The consumptive use of wildlife, including crocodiles, bestows a monetary value on them, and this value increases the likelihood that they will be conserved. This is an important point, because without the consumptive, economically positive use of the natural wildlife resource, livestock expansion could pose a real threat to large parts of Botswana (Simbotwe & Matlhare, 1987b; Barnes, 2001). It has been demonstrated that with effective management of previously exploited crocodile populations, commercial utilization can not only be sustainable, but beneficial to the species (Webb *et al*., 1994).

The collecting of eggs from the Okavango system has decreased the number of small crocodiles in the system, especially in the northern panhandle region, where the presence of a hatchling or yearling animal is now the exception, rather than the rule (Pers. obs, 2005, 2006). Approximately 8 000 eggs, representing over half of those produced in the last four years, have been removed by crocodile ranchers. There has, to date, been no repatriation of wild-originated juveniles. Unfortunately, there is no way of estimating the number of animals killed by indigenous peoples utilizing the river for their livelihood. These people come into contact with crocodiles on a regular basis, and the nature of these interactions is very rarely positive (Thomas, 2006).

2.7 CONCLUSION

Long-lived animals, such as crocodiles, require long-term monitoring to gain accurate long-term demographic trends (Gibbons *et al.*, 2000). Thus, the continued monitoring of the panhandle crocodile population is crucial to effectively manage it.

There have been six categories of factors leading to the global decline of amphibians established by the Partners on Reptile and Amphibian Conservation (PARC, 1999), namely habitat loss and degradation, introduced invasive species, environmental pollution, disease and parasitism, unsustainable use and global climate change. Within the Okavango Delta, introduced invasive species, environmental pollution and disease and parasitism have not yet become an issue as far as reptiles and amphibians go. However, habitat loss and degradation, unsustainable use and global climate change threaten this crocodile population. These issues need to be addressed at the policy-making level, to curb their negative impacts.

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CHAPTER 3:

EVALUATING NOCTURNAL SPOTLIGHT COUNT AND AERIAL SURVEY METHODS FOR THE ESTIMATION OF ABUNDANCE, DISTRIBUTION AND POPULATION TREND-ANALYSIS OF THE NILE CROCODILE, *CROCODYLUS NILOTICUS*, IN THE PANHANDLE REGION OF THE OKAVANGO DELTA, BOTSWANA.

3.1 ABSTRACT

Spotlight counts and aerial surveys have been extensively used to estimate population abundance and elucidate population trends in crocodilian populations around the world. We used these techniques to assess their accuracy and usefulness in the panhandle region of the Okavango Delta, Botswana. Two years of spotlight survey data, including 186 night shifts, yielded 2679 encounters, of which 456 crocodiles submerged before size estimates could be obtained. Spotlight counts revealed a decline in the encounter-rate of crocodiles on the Okavango River with time, although more long-term data needs to be collected to confirm this trend. During the low-water season (September - February), 22.34 % of all crocodiles were observed, while during the flood-season only 13.34 % were observed, yielding correction factors for spotlight surveys for all animals as 4.46 (low - water) and 7.49 (high - water). As far as the adult animals go, spotlight counts located 19.97 % of adults in the low-water period, and 13.37 % in the high-water season, yielding correction factors of 5.0 and 7.5 respectively. Two aerial surveys, conducted at the low-water and high - water peaks yielded total estimates of 588 (77.7 % of adults, low - water) and 350 (56.7 % of adults, high - water) adult crocodiles, yielding correction factors of 1.28 (low - water) and 1.77 (high - water). Aerial and spotlight surveys should therefore be conducted in the low-water season (September - February) to obtain best results for population trend analysis. In addition, correction factors for these estimates should be locally calculated to be accurate.

3.2 INTRODUCTION

3.2.1 The Nile crocodile in the Okavango Delta

The Nile crocodile, *Crocodylus niloticus*, occurs throughout the Okavango Delta in north-eastern Botswana, and the population extends up the Okavango River into Namibia (Kavango River) and Angola (Cuito and Cubango Rivers). A number of human-induced disturbances have lead to the decline of the Okavango crocodile population over the last forty years (Graham *et al*., 1992). These include extensive hide-hunting, habitat destruction, interference from local fishermen and reed-cutters, boat traffic and removal of breeding animals and eggs from the wild by crocodile farmers without the release of juveniles back into the system. Through the late 1950's and up to 1969 when organized hunting ceased, between 12 000 and 48 000 animals were shot by hide-hunters (Pooley, 1982; Graham *et al.*, 1992). From 1983 to 1988 over 1000 live adults were removed from the system by crocodile farmers. In addition, 14 000 eggs were removed between 1983 and 1987 (Graham *et al*., 1992). This led to a 50 % reduction of the breeding population (Simbotwe & Matlhare, 1987). Another 8 000 eggs were removed from the panhandle from 2003 - 2006. The last attempt to assess the number of crocodiles in the population, using aerial survey techniques, yielded an estimate of 10 000 adult crocodiles (Simbotwe & Matlhare, 1987). In 2002, at the commencement of this study, there had been no research conducted on this crocodile population for well over 15 years.

3.2.2 Spotlight surveys

The spotlight method of surveying crocodilians was standardized in 1977 (Messel *et al*., 1977) and has proved to be a very successful and reliable method over the last three decades (Letnic & Connors, 2006). This method is the most frequently employed technique to evaluate crocodilian population trends (Bayliss *et al.*, 1986; Thorbjarnarson *et al.*, 2000; Stirrat *et al.*, 2001; Letnic & Connors, 2006; Combrink *et al.*, in Press). Due to a reflective layer in the eye known as the tapetum lucidum (Grenard, 1991), crocodilian eyes reflect any bright light shone into them and exposed crocodiles can be located for distances in excess of 100 m. Location depends on a number of factors such as vegetation density, the strength of the spotlight and the relative position of the crocodile (Chabreck, 1966; Woodward & Marion, 1978; Hutton & Woolhouse, 1989; Combrink, 2004). Combrink (2004) provides a detailed literature review and description of the spotlight survey method.

Spotlight surveys have traditionally been used to assess and monitor populations by providing the researcher with indices of population size and density (Bayliss *et al.*, 1986; Hutton &

Woolhouse, 1989; Games, 1990; Woodward & Moore, 1993; Ron *et al.*, 1998; Platt & Thorbjarnarson, 2000; Thorbjarnarson *et al.*, 2000; Brown *et al.*, 2004; Letnic & Connors, 2006). However, spotlight counts are inherently inaccurate due to a number of factors causing visibility bias, and observers do not necessarily see all of the crocodiles present during a survey (Bayliss *et al*., 1986). Factors influencing the probability of detection of crocodiles include: the type and structure of vegetation between the observer and the crocodile, river width, frequency of bends (sinuosity), position of the crocodile (submerged, on land etc), the orientation of the crocodile in relation to the observer, and the wariness of the crocodile. Additionally, at any given time, up to 38 % of crocodiles may be underwater (Bayliss *et al*., 1986; Hutton & Woolhouse, 1989). Large crocodilians tend to be more wary than the smaller size classes and often submerge when approached (Webb & Messel, 1979; Ron *et al*., 1998). Spotlight counts therefore represent an index of the total population and without an idea of how many animals there are in the system, there is no way to check on the relationship between spotlight counts and total population size (Woodward & Moore, 1993). However, in conjunction with population estimates, correction factors can be applied to spotlight count data to improve the accuracy thereof. Nevertheless, for trend analysis without the knowledge of population size, the assumption is made that the relationship between total population size and spotlight count density remains constant (Woodward & Moore, 1993).

3.2.3 Aerial surveys

Aerial surveys have proved useful in counting large, visible animals (Samuel *et al*., 1987), having the advantage of allowing access to those areas that are remote or inaccessible, when there are very large areas to survey and counting animals that are difficult to census by other means. Additionally, aerial surveys can be done rapidly, at the same time of year, whereas land-based and boat surveys across many areas take a long time and may cause sighting biases by passing through seasonally significant times such as the peak of winter when the numbers basking are maximized (Bayliss *et al.*, 1986; Webb, Pers. comm, 2007). These surveys have proved useful for surveying crocodilian populations in many cases (Pooley, 1982; Mourao *et al.*, 1994; Coutinho & Campos, 1996). Traditional methods of estimating crocodilian population sizes, namely capture-mark-recapture (Chabreck, 1966; Glastra, 1983; Bayliss *et al.*, 1986; Hutton, 1987a; Hutton & Woolhouse, 1989; Games, 1990; Brandt, 1991) and nocturnal spotlight counting techniques (Chabreck, 1966; Glastra, 1983) may be inaccurate when determining total population estimates in regions that include inaccessible areas if the animals are not all available for censussing. Due to the nature of the wetlands, which flood seasonally (March-August), many of the areas that crocodiles frequent were inaccessible by boat. The use of aerial survey techniques for assessing crocodilian distribution and abundance, and for the

location and mapping of nesting sites, has proved invaluable in areas such as the rivers within the Caprivi strip of Namibia (Brown *et al.*, 2004), Lake Sibaya, South Africa (Combrink, 2004), the Pantanal (Mourao *et al*., 1994) and Florida (Rice *et al.*, 1999). For further studies using aerial survey techniques on crocodilians, see: (Magnusson *et al.*, 1978b; Magnusson *et al.*, 1980; Hutton *et al.*, 1992; Coutinho & Campos, 1996; Stirrat *et al.*, 2001; Harvey & Hill, 2003; Brown *et al.*, 2004; Kay, 2004; Read *et al.*, 2004).

Spotlight and aerial surveys can be used to provide an index of crocodile density, but both methods have inherent biases. Spotlight surveys will not detect animals that are submerged (Bayliss *et al*., 1986) and large animals tend to be more wary than smaller ones (Webb & Messel, 1979). Aerial surveys tend only to be successful for the adult animals in a system, as smaller animals are difficult to detect from the air. Given the constraints of both survey methods it is likely that densities recorded underestimate actual population size (Letnic & Connors, 2006). However, in combination, the trends observed by these techniques provide a relatively cost-effective method for the long term monitoring and management of crocodilian populations (Stirrat *et al*., 2001; Letnic & Connors, 2006).

The aim of this study was to assess the effectiveness of both spotlight and aerial survey techniques compared to the capture-mark-recapture study, and to refine future survey techniques by calculating seasonal correction factors for these data for the panhandle region. The results of two aerial surveys, in which the abundance and distribution of adult Nile crocodiles (total length > 2 m) were assessed, and three years of spotlight surveys conducted in the panhandle region of the Okavango Delta, are presented in this chapter.

3.3 MATERIALS AND METHODS

3.3.1 Study area

The Okavango Delta, an alluvial fan (Mendelsohn & el Obeid, 2004), is the worlds' largest Ramsar site[13] and is situated in the North-eastern region of Botswana, Southern Africa (Figure 12). The panhandle region of the Okavango Delta is approximately 107 km long as the crow flies, and carries the channelled water of the Okavango River until it is discharged into the Delta proper (Figure 13). Annual flooding of the entire system begins in Mohembo (January / February) with the influx of water from the drainage basins in the Angolan highlands discharging into the Kavango River. These flood waters take about six months to reach the southern-most extremities of the Delta due to the very shallow geographical gradient of the system (McCarthy & Ellery, 1998). The Department of Water Affairs recorded daily maximum and minimum water levels (m) at Stations 7134 (Sepopa) and 7112 (Mohembo). During the time period 2004 - 2007, the water level fluctuated at the stations by 3.5 m at the Mohembo station, and by 1.9 m at the Sepopa station. This was accounted for by the narrow floodplain (~ 2 km) at Mohembo, which then becomes wider (10 - 18 km) in the Sepopa region, allowing the water load to spread out downstream from its entrance into Botswana. The permanent, swiftly flowing channels are typically walled by papyrus (*Cyperus* sp.) and tall reeds (primarily *Phragmites australis*), with sandbanks on many of the corners. Due to the elevated banks in the panhandle, created by the deposition of sediments, this region supports 99 % of the Nile crocodile breeding population (Graham *et al*., 1992) in the Okavango Delta.

The data collected upstream and downstream of the upper entrance to the Upper Phillipa (Figure 13) were separated for analysis into the northern and southern panhandle regions. The crocodiles in the upper panhandle region were exposed to higher levels of human-induced disturbance than in the southern region and as early as 1973 there was a natural separation, defined by a scarcity of crocodiles from Redcliffs that ran a distance of approximately 8 km downstream (Taylor, 1973). It was assumed that this influence would have resulted in the animals in the northern panhandle being more wary of people, and thus violating the assumptions of the capture-mark-recapture (CMR) models by altering capture probabilities between the northern and southern panhandle regions (see below). The northern and southern crocodiles did not seem to interact, with only one individual recorded crossing from the north to the south during the study (Chapter 6). The reasons for the persistent lack of crocodiles in this region remain unknown.

[13] Ramsar – wetlands of international importance.

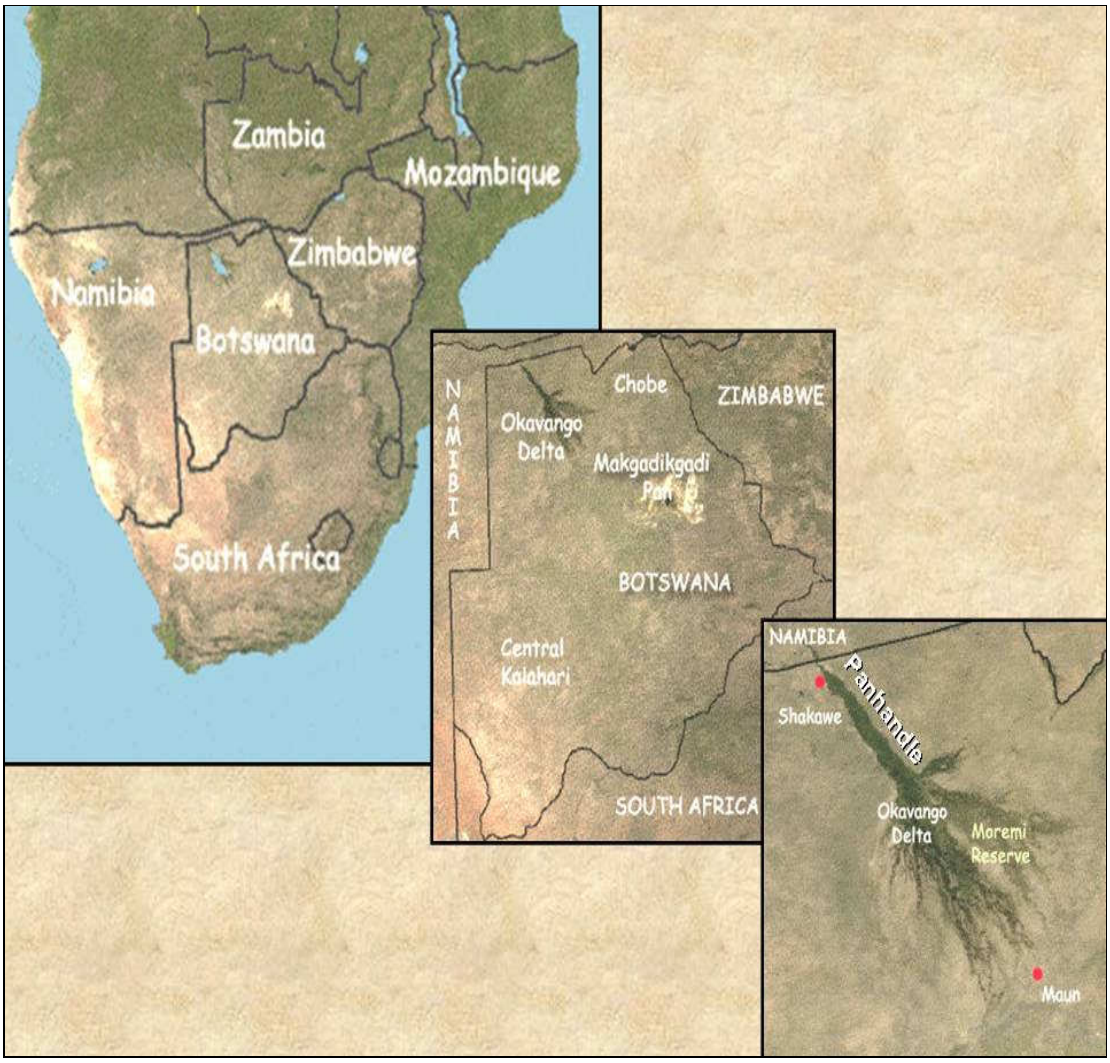

Figure 12. The study area in the panhandle region of the Okavango Delta, Botswana (source: **http://www.egnu.com/maps/okavango_map.html**, accessed on 28/07/07).

3.3.2 Spotlight Surveys

Four spotlight counts were conducted between Seronga in the southern panhandle and the Botswana / Namibia border at the northern-most point of the Okavango River in Botswana (Table 8). During these surveys, accessible channels and lagoons were surveyed together with the main channel. These discrete spotlight counts were conducted as part of the mark-recapture study in the area and specifically tested for seasonal differences in crocodile densities. As such, the surveys were conducted in February 2005 and 2006 (flood-season) and August 2005 and October 2006 (low-water season). The spotlight counts were, however, not limited to these four sessions. Between June 2004 and October 2006, all crocodiles encountered during the nocturnal surveys (n = 189) were recorded, whether or not they were captured, to determine accurate size-class distribution and abundance. While use was made of Earthwatch volunteers, there was always a trained and experienced team member checking their performance whilst searching for

a crocodile to capture. All the spotlight data collected during these surveys were pooled to obtain average size-class ratios for the Okavango River.

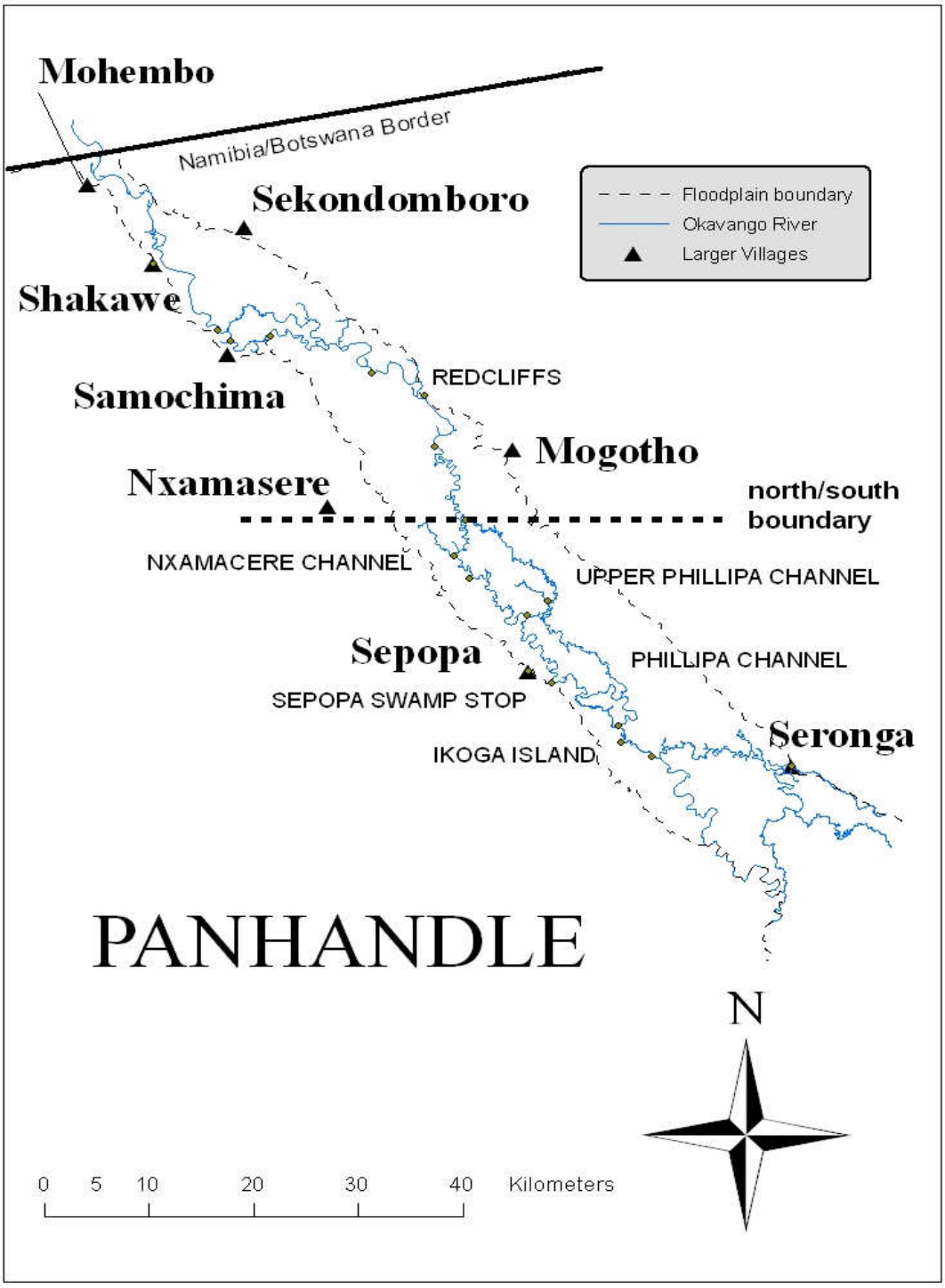

Figure 13. The panhandle region of the Okavango Delta, Botswana, showing the extent of the "northern" and "southern" research areas.

Nocturnal spotlight surveys were conducted between 20h00 and 04h00. Crocodiles were located at night from a 5.8 m flat-bottomed aluminum boat using a 12 volt, 500 000 candle-power spotlight. A team of four to six boat crew members were used, including one trained observer with at least one years' spotlighting experience at the front of the boat. The boat cruised at an average speed of 8 – 10 $km.hr^{-1}$ (Hutton & Woolhouse, 1989), while the spotlight beam was traversed through an arc of 180^0, illuminating the river banks, the water-vegetation interface, and the main river channel. Each observer was changed at 30 minute intervals to reduce fatigue. When eye shine (i.e. a crocodile) was observed, speed was reduced to minimise disturbance and improve manoeuvrability. The crocodile was approached, captured where possible and processed as part of the mark-recapture study (Chapter 3). If the individual submerged, or was too large to handle from the boat (> 3.5 m), its total length was estimated by multiplying the estimated head length of the crocodile by a factor of 7 (Hutton, 1987b). When a crocodile submerged before the observers were close enough to reliably estimate its length, it was recorded as an "eyes only" observation. Each crocodile's locality was recorded using a Magellan 301 S global positioning system (GPS), and plotted on a map using ArcGIS v. 9 (ESRI, 2006). Water and air temperature was recorded at the time of capture of each crocodile during the surveys using a BATT-12 thermocouple meter (Physi-temp, CA, USA) and a Cu – Cn thermocouple probe of 1500 mm in length. Water temperature was measured approximately 400 mm below the surface, off the side of the boat.

I. Analyses

Crocodiles were divided into five size classes to determine size specific densities. The various size classes demonstrate behavioural differences, in that larger crocodiles are more wary (Webb *et al.*, 1982; Webb *et al.*, 1983; Hutton, 1989; Kofron, 1993) and ecologically, in that crocodiles of different sizes separate themselves spatially (Games, 1990; Leslie, 1997; Kay, 2004; Wallace & Leslie, in Press). A size class separation was therefore logical from an analytical point of view (Polis, 1984). The size classes were (measurements in mm, snout-vent length): Hatchlings, < 169, Yearlings, 170-389, Juveniles, 390-663, subadults 664-1158, Adults > 1159. These size classes approximately follow those of previous and concurrent southern African studies (Games, 1990; Leslie, 1997; Wallace & Leslie, in Press).

Spearman rank order correlations for non-parametric data were performed using Statistica v. 7.1 (StatSoft, 2006) to determine the relationship between average monthly and annual *C. niloticus* densities and seasonal effects, including the effects of water level, air and water temperature. The absolute numbers of crocodiles encountered were *Ln*-transformed (Eberhardt, 1978; Woodward

& Moore, 1993) prior to performing formal regression trend analyses to avoid violating the assumptions of linear regressions or trend analyses.

3.3.3 Aerial surveys

Two aerial surveys were undertaken, the first from 30 June - 11 July 2005 (height of flood) and the second from 5 January - 13 January 2006 (low - water) to estimate the total adult (> 2 m TL) population of Nile crocodiles in the panhandle. The panhandle was divided into 19 sample blocks, each 3 km apart and 1.2 km in width, with long axis in an east-west direction across the floodplain (Figure 15). The sample represented 30 % of the entire panhandle region and was designed to maximise the area covered and represent any areas of differing crocodile densities equally.

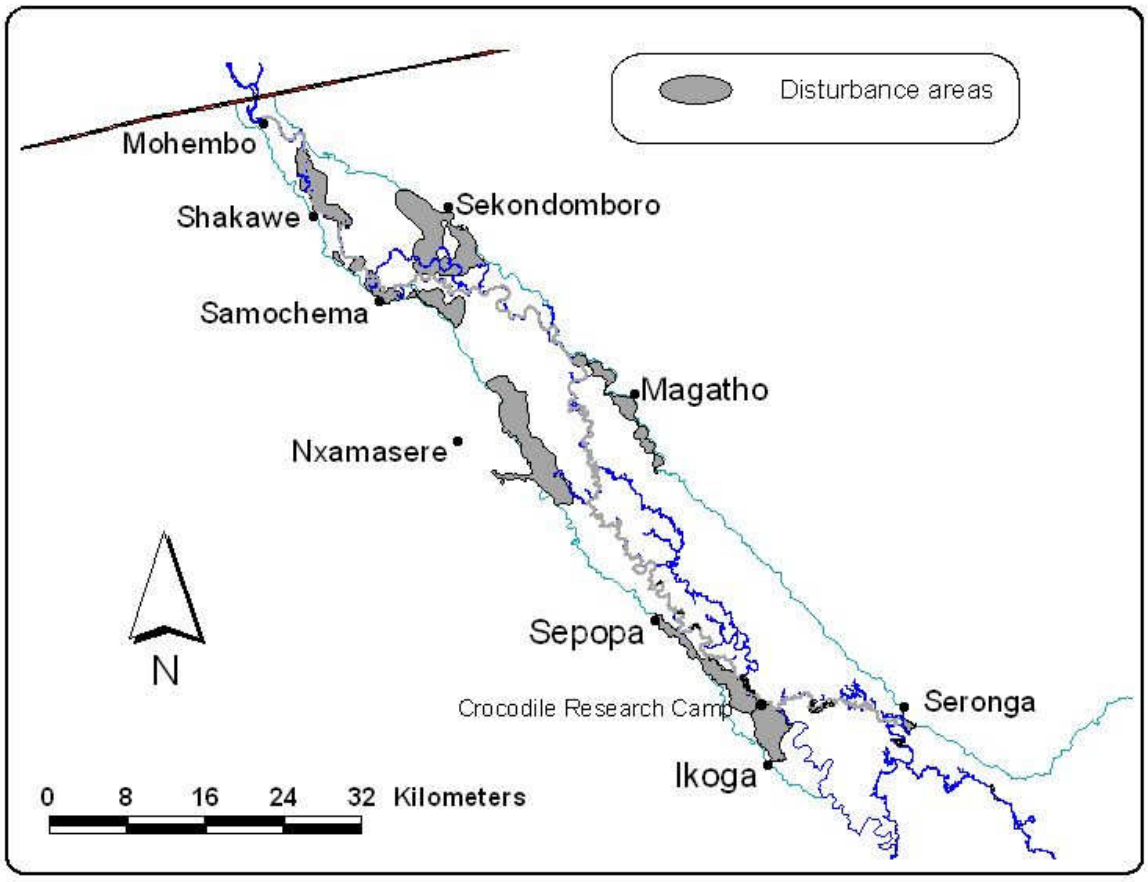

Figure 14. A map of the panhandle area of the Okavango Delta, showing areas of human disturbance. Human disturbance included: fire, lodges, boat traffic and cattle grazing. The northern region of the panhandle, where annual egg-harvesting took place, suffered more human-induced disturbance and disruption to the size class distribution than the relatively undisturbed southern section (Shacks, 2006).

Transect lines were orientated east-west to maximise the habitat types in the sample so as not to over-represent the main Okavango River channel that flows north-west to south east (Craig & Gibson, 1995). Within each sample block, parallel flight lines spaced at 200 m intervals ensured total coverage of the sample block (Figure 16). Crocodiles observed up to an estimated distance of 100 m on either side of each transect line were counted by two experienced observers, one on each side of the aeroplane. All adult crocodiles were counted in each of the 19 blocks from a Cessna 206 (survey 1) and a Cessna 172 (survey 2) aeroplane. An altitude of 100 – 110 m was maintained with a ground speed of 100 - 130 km/hr^{-1}. The altitude and speed were carefully regulated, and were selected to maximise the number of crocodiles seen basking within the 100 m strip on either side of the aeroplane. Surveys were conducted for not more than three hours (excluding travel time) per session to avoid observer fatigue. The surveys were flown on clear, windless days between 08h30 and 11h30 when the adults were basking. Care was taken not to double-count any animals, and if there was a chance of an observed animal being counted twice (from recorded GPS points), the second observation was excluded from the data set. Two Garmin III+ GPS units were used, one to orientate the pilot and to track the flight path and the other to record the co-ordinates of each observed animal.

I. Analyses

The total count data were downloaded and saved daily using Garmin's Mapsource software. Population density and variance within the panhandle was estimated for sampling blocks of unequal size (Jolly, 1969), as follows:

$$R = \frac{\sum_{i=1}^{n} y1}{\sum_{i=1}^{n} z1}.$$

$$Y = Z.R$$

$$\mathbf{V} = \frac{N(N-n)}{n}.(S_y^2 - 2.R.s_{zy} + R^2.s_z^2)$$

Where:

R = density of animals

Y = total number estimated

y_i = number of animals counted in transect

z_i = area of transect

n = number of transects possible in stratum

Where: $$N = \frac{n.Z}{\sum_{i=1}^{n} Z_i}$$

S_y^2 = variance of number seen per transect

S_z^2 = variance of transect area

S_{zy} = covariance between number seen per transect and transect area

V = variance of estimated number in stratum (i.e. variance of Y)

Overall densities and standard errors were obtained from sums of the stratum densities and their variances (Craig & Gibson, 1995).

One sample block ("R" block) was removed from the analysis as it was not possible to fly it during the second survey due to the presence of military aircraft. A t-test for dependent samples was performed on the densities for each block, to test for differences between the seasons.

3.3.4 Correction factors

Both aerial and spotlight surveys are inherently biased and the methods tend to under-estimate the true population size. The reliability of the population estimates obtained depend on factors such as water level, vegetation cover and various other factors that conceal crocodiles during surveys (Bayliss *et al*., 1986).

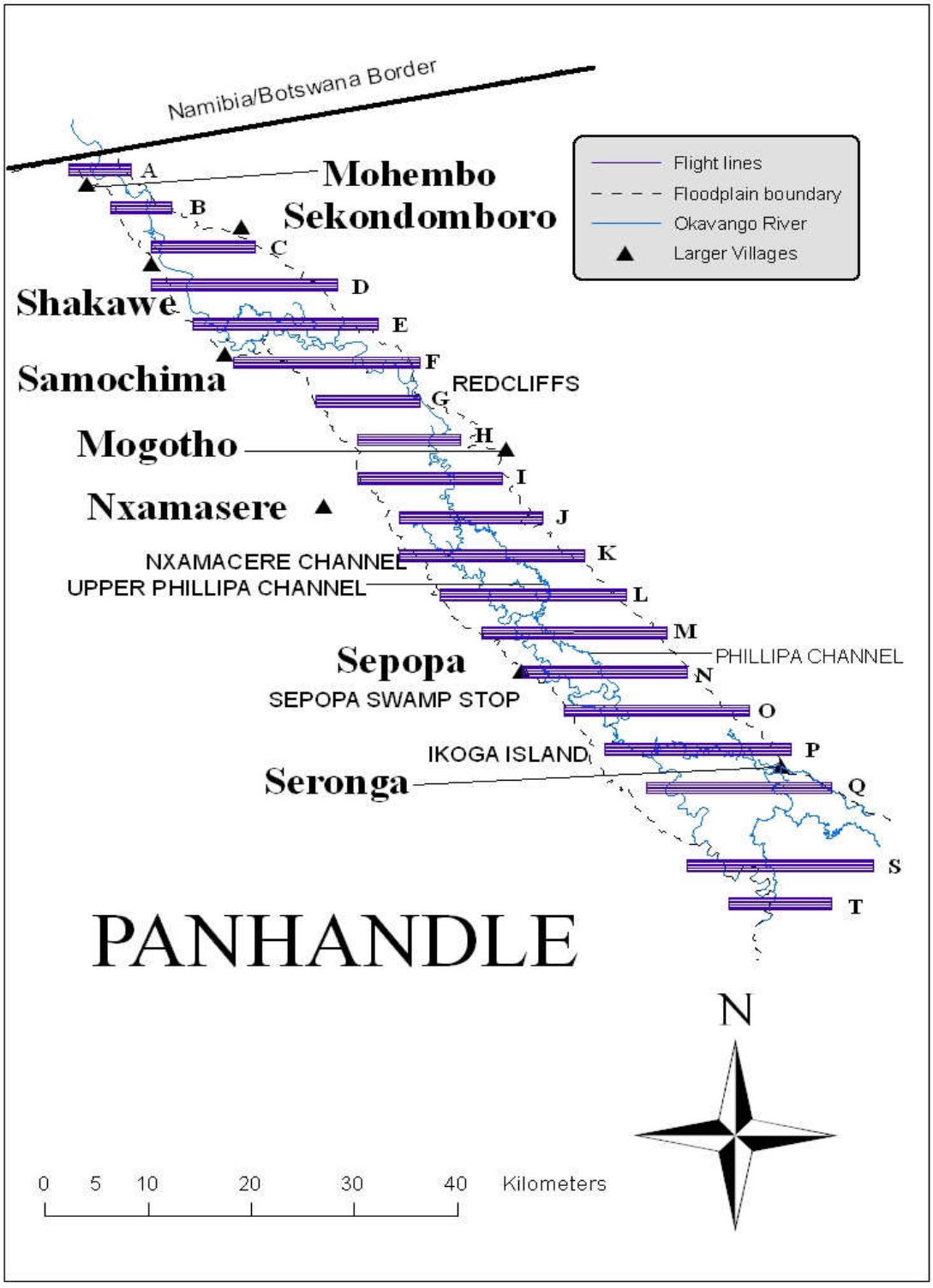

Figure 15. A diagram showing the flight tracks used during the aerial surveys, crossing the panhandle floodplain. Within each block there were six flight tracks, spaced at 200 m intervals.

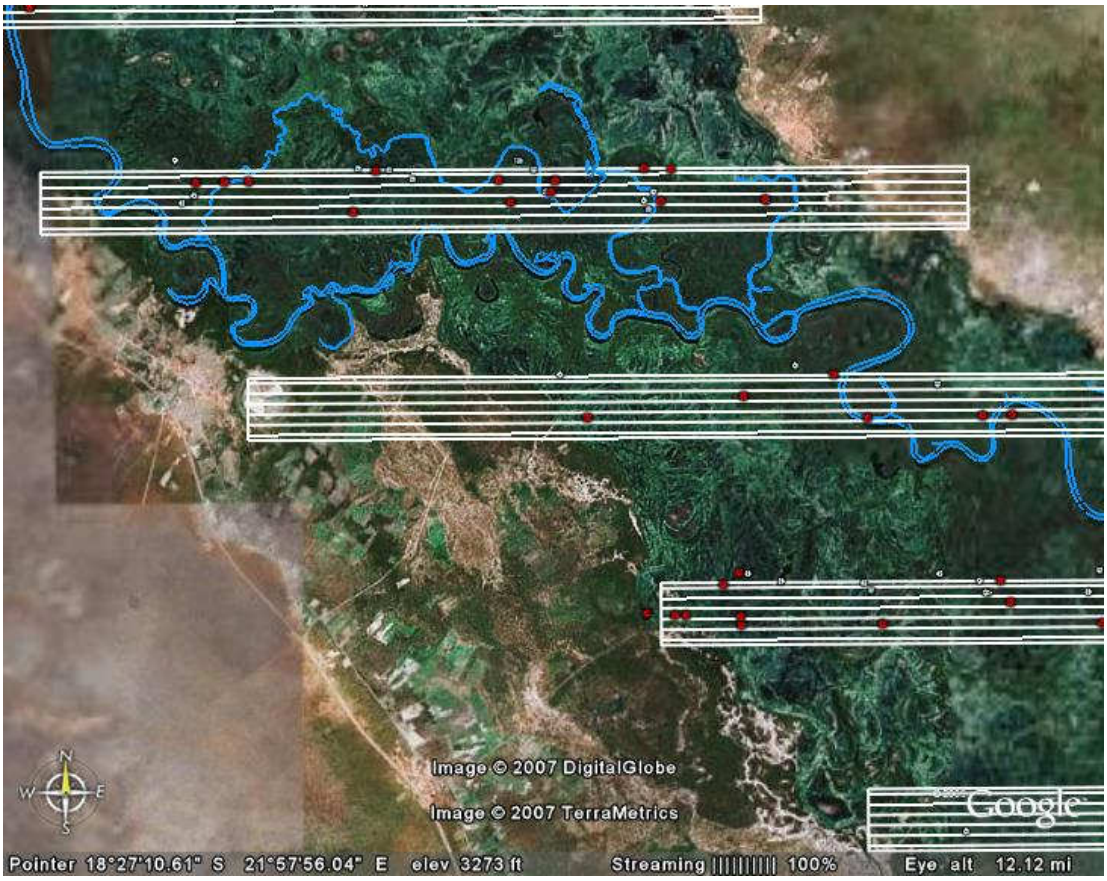

Figure 16. Expanded view of (from top, including partially illustrated) flight blocks D - H (see Figure 15). Total counts were conducted in each block. The dots illustrate GPS crocodile sightings as recorded by the GPS units.

To estimate an accurate population size of crocodilians using either of the above survey methods, correction factors are normally calculated and applied to the data (Bayliss *et al*., 1986; Hutton & Woolhouse, 1989). While correction factors are advocated for crocodilian aerial surveys to account for the animals missed by observers (Magnusson *et al*., 1978a; Stirrat *et al*., 2001), the areas surveyed were open expanses of wetland, and it was therefore assumed that crocodiles would be clearly visible while basking. Seasonal correction factors were calculated as the degree to which the aerial survey estimates differed from the capture-mark-recapture adult population estimates obtained during this study (Chapter 2), i.e. by dividing the average panhandle adult population, estimated from CMR data, by the number of adults estimated from aerial survey data. This assumed that adult crocodiles that were counted in the aerial surveys were moving back to the main channel and were accessible to the research team during the capture-mark-recapture experiment.

The spotlight count data were divided into low - water (September-February) and high - water (March-August) periods to calculate separate seasonal correction factors for the spotlight-based population estimates. The correction factors were calculated by dividing the average annual population estimate obtained from the CMR experiment (Chapter 2) by the seasonal spotlight count estimates.

3.4 RESULTS.

3.4.1 Spotlight surveys

A total of 2679 crocodiles were encountered in the panhandle from 186 nocturnal surveys between June 2004 and October 2006, of which 456 (17 %) were “eyes only”, submerging before size estimates were obtained. Of the animals for which size estimates were obtained, a total of 18 were hatchlings (0.7 %), 714 were yearlings (26.7 %), 431 were juveniles (16.1 %), 417 were subadults (16.0 %) and 643 were adults (24.0 %). Hatchlings made up a very small proportion of the encounters and were therefore not included in any further density-based analyses. The crocodile encounter rate increased during the months when water levels were low (SROC = 0.67, $p < 0.05$), and was highest between September and February.

There were no significant seasonal differences in the densities of animals during the four discrete spotlight surveys, either within size classes (t-test, $p > 0.26$) or for the population as a whole (t- test, $p = 0.83$) (Table 7). These data were therefore included with data collected over the entire two year period, and analysed as part of this dataset.

Monthly encounter rates for the whole panhandle generally decreased with increasing crocodile size for the yearling (0.28 individuals.km^{-1}), juvenile (0.19 individuals.km^{-1}) and subadult size classes (0.12 individuals.km^{-1}) (Figure 17, Table 8). The adult size class (0.19 individuals.km^{-1}), shared the second highest encounter rate with the juvenile size class.

There were no statistically significant differences in size-class specific densities between the northern and southern panhandle regions (Mann-Whitney U tests, $p > 0.05$, Figure 18, Table 8). However, although not significant general trends suggested that densities in all size classes were marginally higher in the southern panhandle, with the exception of subadult animals that appeared to be more abundant in the northern panhandle (0.17 individuals.km^{-1} ± 0.05) than in the southern panhandle (0.11 individuals.km^{-1} ± 0.03).

Table 7. T-test results from four discrete spotlight surveys comparing size-class densities from high-water (February 2005 / 2006) and low-water (August 2005 / October 2006). No significant differences in densities were observed between size classes, for the population as a whole, or between seasons.

	Mean high-water encounter rates (crocodiles.km^{-1})	Mean low-water Encounter rates (crocodiles.km^{-1})	t-value	df	p
Eyes only	0.15	0.19	-0.28	2.00	0.81
Hatchlings	0.03	0.00	1.00	2.00	0.42
Yearlings	0.37	0.28	0.64	2.00	0.59
Juveniles	0.14	0.15	-0.27	2.00	0.81
Subadults	0.11	0.17	-0.49	2.00	0.67
Adults	0.13	0.22	-1.58	2.00	0.26
Total encounter rates	0.93	1.00	-0.24	2.00	0.83

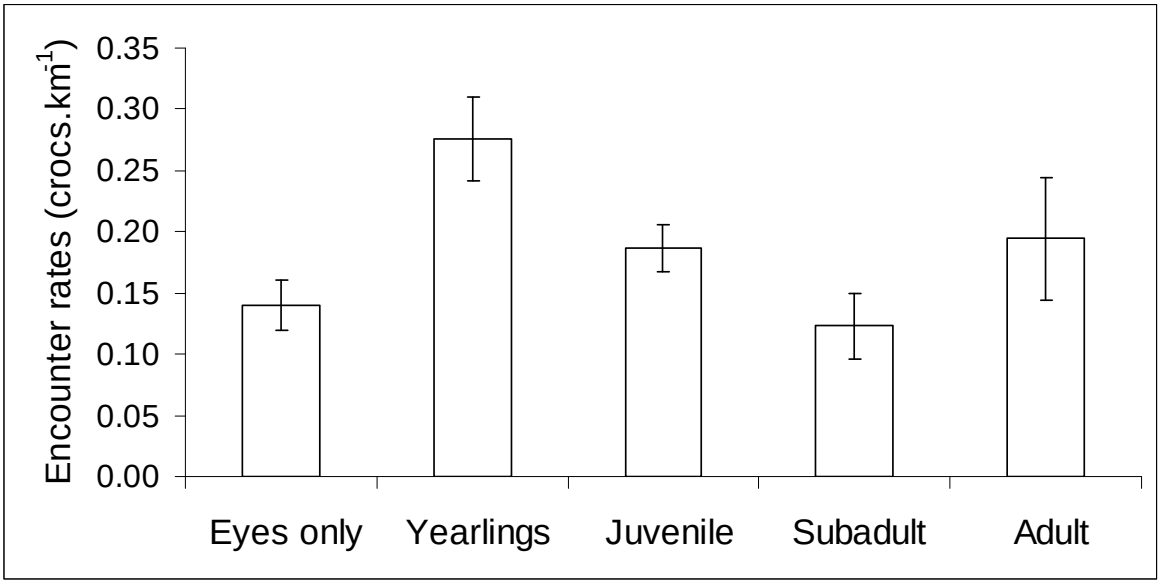

Figure 17. Graphic representation of the harmonic means (monthly) of encounter rates for all observed crocodiles in the panhandle, categorized by size-class. The size classes were (measurements in mm, snout-vent length): Hatchlings, < 169, Yearlings, 170 - 389, Juveniles, 390-663, Subadults 664-1158, Adults > 1159. These size classes follow those of Leslie (1997) and Wallace (2006).

Table 8. Descriptive statistics for mean monthly encounter rates with crocodiles throughout the panhandle from June 2004 - October 2006, divided into northern and southern regions. The harmonic mean was calculated with associated standard errors (Stirrat *et al*., 2001).

Region	Encounter rate (ind.km^{-1})	N (months)	Harmonic Mean (animals.km^{-1})	Min	Max	SE Harmonic mean
Entire panhandle	Total	30	1.19	0.57	4.23	0.11
	Eyes only	29	0.14	0.00	0.65	0.02
	Yearlings	30	0.28	0.09	1.76	0.03
	Juvenile	30	0.19	0.09	1.71	0.02
	Subadult	30	0.12	0.02	0.61	0.03
	Adult	30	0.19	0.02	1.03	0.05
Southern panhandle	Total	19	1.24	0.65	4.23	0.14
	Eyes only	19	0.14	0.05	0.48	0.03
	Yearlings	19	0.33	0.17	1.76	0.04
	Juvenile	19	0.22	0.11	1.71	0.03
	Subadult	19	0.11	0.02	0.55	0.03
	Adult	19	0.23	0.11	1.03	0.03
Northern panhandle	Total	11	1.12	0.57	2.55	0.18
	Eyes only	10	0.14	0.00	0.65	0.05
	Yearlings	11	0.22	0.09	0.59	0.05
	Juvenile	11	0.15	0.09	0.34	0.02
	Subadult	11	0.17	0.05	0.61	0.05
	Adult	11	0.16	0.02	0.84	0.09

I. Temporal encounter patterns

A. Spearman rank order correlations (SROC)

The total annual untransformed encounter rates of observed crocodiles in the panhandle decreased significantly with time in years (SROC = -0.43, $p < 0.05$). The overall densities of all individual size classes significantly ($p < 0.05$) decreased with time (yearlings SROC = -0.41, juveniles SROC = -0.37, subadults SROC = -0.38, adults SROC = -0.46).

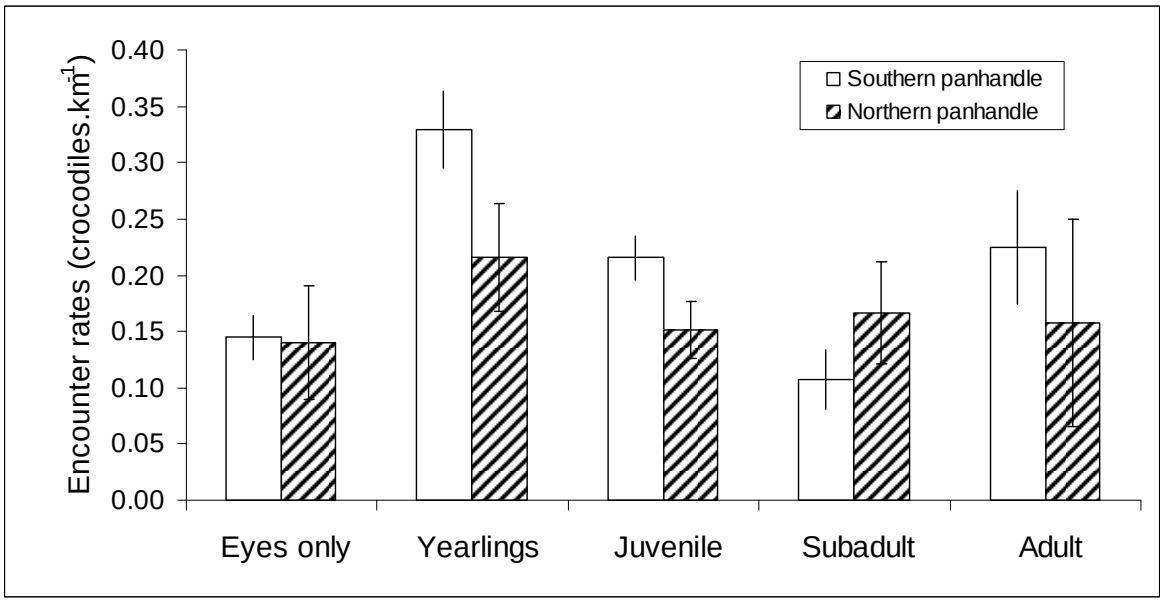

Figure 18. Graphic illustration of the densities of crocodiles of each size class, from June 2004 - October 2006, in the northern and southern panhandle regions. There were no significant differences in size class specific encounters between the two regions (Mann-Whitney U tests, $p > 0.05$).

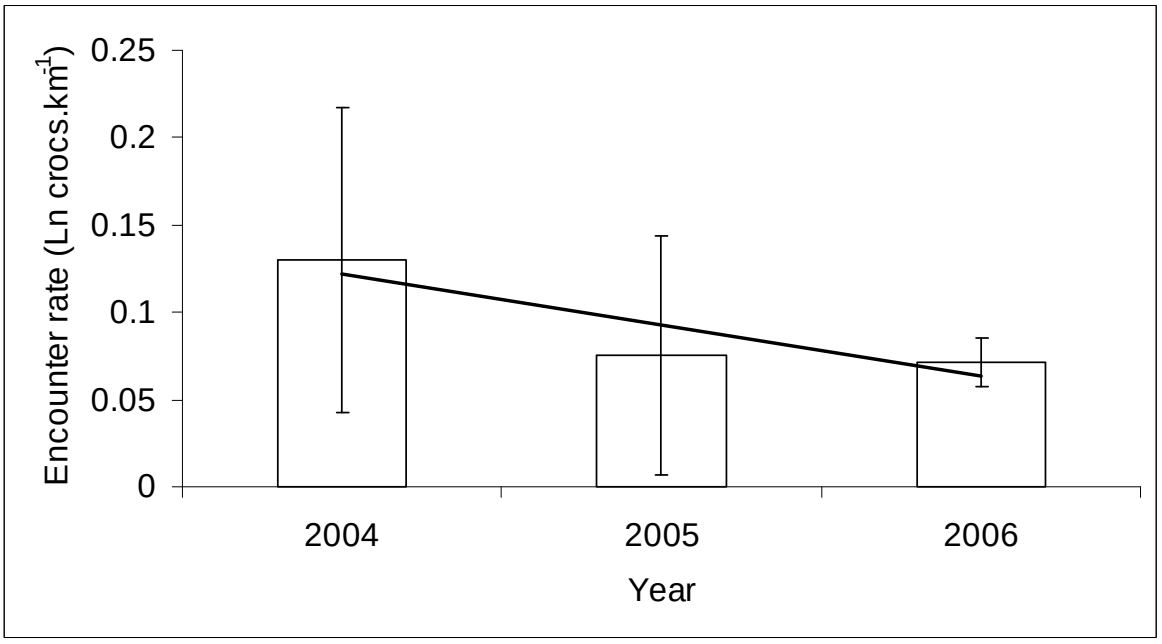

Figure 19. Graphical representation of the *ln*-transformed number of crocodiles encountered during spotlight surveys in 2004, 2005 and 2006.

B. Regression analyses

When analysed using the least-squares regression method, the numbers of crocodiles observed were *ln* transformed before calculating encounter rates to satisfy regression assumptions. Again, encounter rates were negatively correlated with time (in years, Figure 19). Yearlings (β = -0.04, p = 0.1) and juveniles (β = -0.04, p = 0.23) did not correlate significantly with time, while subadults (β = -0.04, p = 0.04) and adults (β = -0.04, p = 0.00) did correlate significantly with time (Table 9).

In the southern panhandle, only encounters with subadults (β = -0.04, p = 0.03) and adults (β = -0.05, p = 0.01) decreased significantly with time. The northern panhandle encounters yielded similar results, with all size classes combined (β = -0.11, p = 0.04), and adults (β = -0.05, p = 0.07), decreasing significantly with time. While other size classes showed the same trend of decreasing encounters with time in both the northern and southern panhandle, these trends were not significant at the p = 0.05 level (Table 9).

II. Crocodile encounters associated with water level

A. Spearman rank order correlations (SROC)

Water level was the single most important environmental factor influencing the encounter rate of crocodiles observed, with the notable exception of the yearling size class. Within the entire panhandle (SROC = -0.64) and within the southern and northern panhandle regions (SROC = -0.66), encounter rates were strongly and negatively correlated ($p < 0.05$) with increasing water level (Table 10).

B. Regression analyses

Over the entire panhandle, the number of crocodiles encountered was significantly, negatively correlated with increasing water levels (Figure 20, Table 11). Within the size classes over the entire panhandle, only yearlings (β = -0.1, p = 0.04), and adults (β = -0.08, p = 0.23) showed significant water-level density-dependence, with the density of animals decreasing with increasing water level (Table 11). While juveniles and subadults exhibited trends of decreasing encounter rate with increasing water level (juveniles, β = -0.13 p = 0.06; subadults, β = -0.03 p = 0.10), these regressions were non-significant. It was suspected that there were relocations of juvenile crocodiles from other areas of the panhandle into the Nxamacere channel over a fairly

long period of time, and this was reflected in the high encounter rates during the low-water season when the Nxamacere channel was surveyed (Table 9, Figure 20). However, in the absence of direct proof of these relocations, these data were included in the results.

When divided into the northern and southern panhandle regions, results differ slightly. In the south, the overall trend is not significant. Yearlings ($\beta = -0.13$, $p = 0.04$), and adults ($\beta = -0.07$, $p = 0.02$) showed a significant decrease in encounter rate with increasing water level while juveniles ($\beta = -0.14$, $p = 0.14$) and subadults ($\beta = -0.04$, $p = 0.13$) did not. In the northern panhandle, only juveniles ($\beta = -0.07$, $p = 0.05$) significantly exhibited the trend of decreasing encounter rate with increased water levels (Table 11).

III. Crocodile encounter rates associated with water temperature

Water temperature did not have a significant effect on the encounter rates with crocodiles in the river, but was significantly correlated to water level (SROC = -0.48, $p < 0.05$).

Table 9. Results for the regressions of transformed total and size-class encounter rates against time (years) for the spotlight surveys. Results include the entire panhandle and the northern and southern regions separately for all size classes with the exception of hatchlings. Significant values are emphasised in bold text.

Region	Size-class	Slope	SE slope	Intercept	SE intercept	n	SE regression	R	p
Panhandle	All	**-0.13**	0.06	**0.57**	0.12	**30**	**0.22**	**0.41**	**0.03**
	Yearlings	-0.04	0.03	0.23	0.06	30	0.10	0.30	0.10
	Juveniles	-0.04	0.04	0.20	0.08	30	0.14	0.22	0.23
	Subadults	**-0.02**	**0.01**	**0.12**	**0.02**	**30**	**0.04**	**0.38**	**0.04**
	Adults	**-0.05**	**0.01**	**0.21**	**0.03**	**30**	**0.05**	**0.54**	**0.00**
Southern panhandle	All	-0.14	0.09	**0.62**	0.19	19	0.26	0.36	0.13
	Yearlings	-0.06	0.04	**0.27**	0.09	19	0.12	0.30	0.20
	Juveniles	-0.08	0.06	**0.28**	0.13	19	0.17	0.29	0.22
	Subadults	**-0.04**	0.02	**0.15**	0.03	19	0.04	0.51	**0.03**
	Adults	**-0.05**	0.02	**0.21**	0.04	19	0.05	0.55	**0.01**
Northern panhandle	All	**-0.11**	0.05	**0.48**	0.11	11	0.12	0.62	**0.04**
	Yearlings	-0.02	0.02	**0.16**	0.04	11	0.05	0.43	0.19
	Juveniles	0.00	0.01	0.07	0.03	11	0.04	0.06	0.87
	Subadults	-0.01	0.01	**0.09**	0.03	11	0.03	0.15	0.67
	Adults	**-0.05**	0.02	**0.22**	0.05	11	0.06	0.56	**0.07**

Table 10. Spearman rank order correlation coefficients, illustrating the effect of increasing water level on untransformed crocodile encounter rates throughout the panhandle and within the northern and southern regions. Correlations that were significant at p = 0.05 are emphasised in bold text.

Region	Yearling density	Juvenile density	Subadult density	Adult density	Total density
Panhandle	-0.26	**-0.53**	**-0.44**	**-0.50**	**-0.64**
Southern panhandle	-0.38	**-0.49**	-0.41	**-0.55**	**-0.66**
Northern panhandle	0.05	**-0.70**	-0.49	**-0.60**	**-0.66**

IV. "Eyes only" encounter rates

"Eyes only" encounters varied from 13.4 - 22.5 % of animals observed on the night-shifts, with the highest overall proportions of eyes only observations in 2006. Within the entire panhandle, the number of animals submerging before size estimates could be obtained was positively and significantly related to encounters observed for all size classes (SROC = 0.75). When divided into their respective size classes, juveniles (SROC = 0.39) subadults (SROC = 0.65) and adults (SROC = 0.64) significantly correlated to the number of "eyes only" observations. Similar results were obtained for both the northern and southern panhandle regions. In the northern panhandle, the encounter rate of all individuals correlated with the number of eyes only observations (SROC = 0.92), as did the juveniles (SROC = 0.64) subadults (SROC = 0.65) and adults (SROC = 0.75).

Table 11. Results for the regressions of transformed total and size-class encounters against area-specific water levels (m) for the spotlight surveys. Water level values for the northern panhandle were obtained from Shakawe and those for the southern region from Sepopa. Results include the whole panhandle and the northern and southern regions separately for all size classes with the exception of hatchlings. Significant values are emphasised in bold text.

Region	Size-class	Slope	SE slope	Intercept	SE intercept	n	SE regression	R	p
Entire panhandle	All	**-0.22**	0.10	**0.65**	0.17	29	0.22	0.37	**0.04**
	Yearlings	**-0.10**	0.05	**0.30**	0.07	29	0.10	0.38	**0.04**
	Juveniles	-0.13	0.06	**0.31**	0.10	29	0.14	0.36	0.06
	Subadults	-0.03	0.02	**0.13**	0.03	29	0.04	0.31	0.10
	Adults	**-0.08**	0.03	**0.23**	0.04	29	0.06	0.49	**0.01**
Southern panhandle	All	-0.25	0.17	**0.73**	0.22	18	0.26	0.43	0.08
	Yearlings	**-0.13**	0.05	**0.36**	0.09	18	0.11	0.49	**0.04**
	Juveniles	-0.14	0.03	**0.35**	0.14	18	0.17	0.36	0.14
	Subadults	-0.04	0.04	**0.14**	0.04	18	0.05	0.37	0.13
	Adults	**-0.07**	0.07	**0.22**	0.05	18	0.06	0.53	**0.02**
Northern panhandle	All	-0.07	0.17	0.36	0.27	11	0.16	0.13	0.15
	Yearlings	0.04	0.05	0.04	0.08	11	0.05	0.25	0.46
	Juveniles	**-0.07**	0.03	**0.18**	0.05	11	0.03	0.60	**0.05**
	Subadults	-0.01	0.04	0.09	0.06	11	0.03	0.08	0.80
	Adults	-0.10	0.07	**0.28**	0.11	11	0.06	0.45	0.16

In the southern panhandle, encounter rate correlated with number of eyes only observations (SROC = 0.65), as did juvenile (SROC = 0.22) subadult (SROC = 0.73) and adult (SROC = 0.67) densities. In no instances were yearling encounters correlated with eyes only encounters. The general trend was increased wariness with size. In the northern panhandle the number of eyes only encounters increased significantly with an increase in water level (SROC = 0.71). These results were confirmed through regression analyses (Table 12). Overall, the number of eyes only observations increased with subadult ($\beta = 1.49$, $p = 0.00$) and adult ($\beta = 0.13$, $p = 0.00$) densities. In the north, the number of eyes only observations increased with overall encounters ($\beta = 0.99$, $p = 0.02$) and the encounters with adults ($\beta = 2.38$, $p = 0.01$) (Table 12). In the south, the number of eyes only observations once again increased with increasing subadult ($\beta = 1.49$, $p = 0.01$) and adult ($\beta = 0.99$, $p = 0.02$) encounter rates.

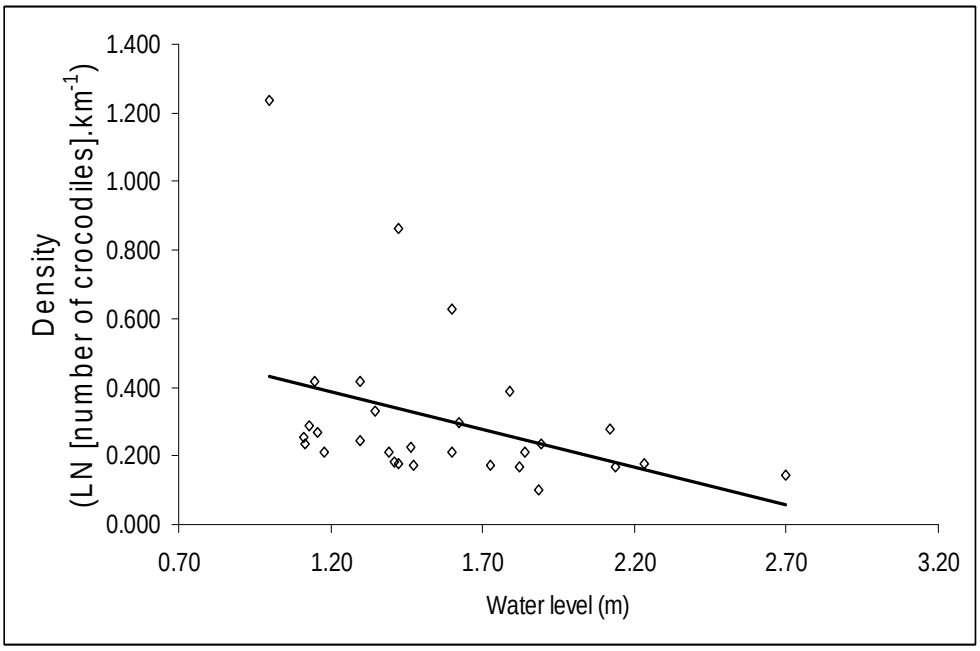

Figure 20. The effect of water level on the encounter rate for all crocodiles encountered in all accessible channels within the panhandle. Absolute numbers were *Ln*-transformed to comply with the assumptions made by regression techniques.

Table 12. Regression results for spotlight-observed animals that were encountered but submerged before size estimates could be made ("eyes only") against all individuals and specific size classes in the panhandle. Significant values are emphasised in bold text.

Region	Size-class	Slope	SE slope	Intercept	SE intercept	n	SE regression	R	p
Panhandle	All	0.05	0.04	0.07	0.02	29	0.05	0.22	0.25
	Yearlings	0.03	0.03	0.07	0.02	29	0.05	0.18	0.36
	Juveniles	0.02	0.03	0.08	0.01	29	0.05	0.13	0.49
	Subadults	**0.19**	0.05	**0.04**	0.02	29	0.05	0.56	**0.00**
	Adults	**0.13**	0.04	**0.04**	0.01	29	0.04	0.59	**0.00**
Southern panhandle	All	0.08	0.12	0.20	0.05	18	0.14	0.17	0.5
	Yearlings	0.07	0.27	0.22	0.05	18	0.14	0.06	0.79
	Juveniles	0.05	0.19	0.22	0.04	18	0.14	0.07	0.78
	Subadults	**1.49**	0.53	**0.12**	0.05	18	0.11	0.56	**0.01**
	Adults	**1.12**	0.45	**0.12**	0.05	18	0.12	0.52	**0.02**
Northern panhandle	All	**0.99**	0.33	**0.00**	0.10	11	0.16	0.71	**0.02**
	Yearlings	1.71	1.35	0.08	0.15	11	0.20	0.39	0.24
	Juveniles	2.57	1.72	0.09	0.13	11	0.20	0.45	0.17
	Subadults	0.83	2.11	0.19	0.18	11	0.22	0.13	0.70
	Adults	**2.38**	0.67	**-0.03**	0.09	11	0.14	0.76	**0.01**

3.4.2 Aerial surveys

A total flying time of 35 hours was required to complete both surveys, and 105 and 144 adult Nile crocodiles were counted in the 2005 and 2006 surveys respectively, in a total sample area of 331.2 km^2. This yielded an estimate of 380 adult crocodiles ± 22 % (CI) in the 2005 survey with an average density 0.34 animals/km^2 ± 0.23, and 521 adult crocodiles ± 17 % (95 % CI) with an average density 0.44 crocodiles/km^2 ± 0.23 for the 2006 survey.

A t-test for dependent samples did not show a significant seasonal difference ($p > 0.05$) between the two surveys (Figure 21) The highest densities of animals were recorded in the northern reaches of the panhandle in the Redcliffs region (G block; mean = 0.96 adults.km^{-1}), Mohembo (B Block; mean = 0.76 adults.km^{-1}, n = 2) and Kgala Thaoga (E block; mean = 0.63 adults.km^{-1}) areas (Figure 21). A low density of crocodiles was found in the Shakawe region (D Block; mean = 0.25 adults.km^{-1}) and the region between Nxamacere and Redcliffs (Blocks H - K; median = 0.18 adults.km^{-1}), an historically low-density region (Taylor, 1973). Medium densities were recorded from Sepopa to Seronga (Blocks M - P; median value = 0.34 adults.km^{-1}) (Figure 21).

Adult crocodiles occurred at higher densities in the Upper and Lower Phillipa channels and in the floodplains to the east of the main channel (Figure 22).

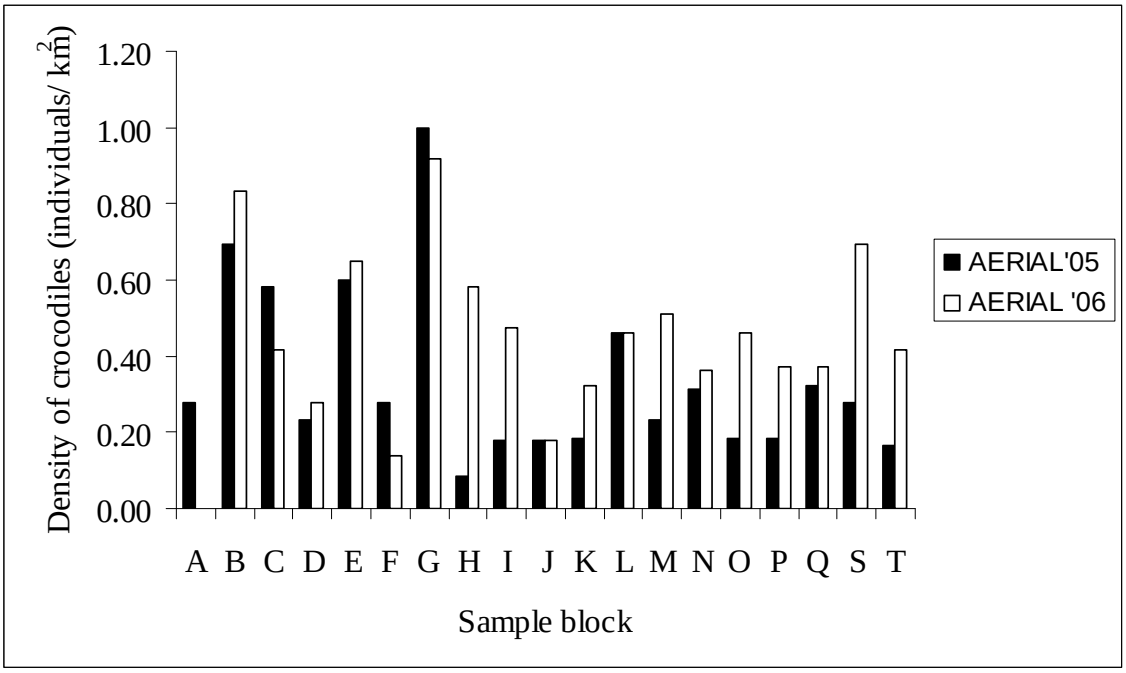

Figure 21. The densities of adult crocodiles counted during the aerial surveys in 2005 and 2006 per sample block. Blocks A-T lie from Mohembo in the North to the region where the alluvial fan of the Okavango Delta begins.

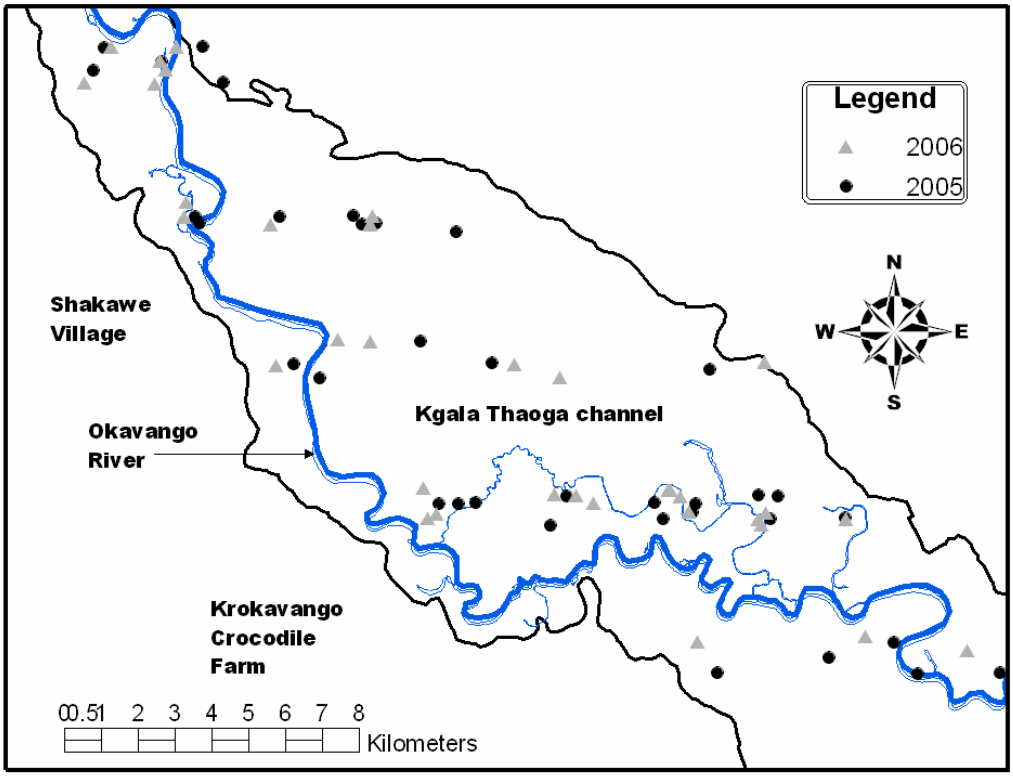

Figure 22. The region covering Shakawe village and the Kgala Thaoga channel area of the northern panhandle, with individual adult crocodiles observed during both aerial surveys represented by the symbols. Only the main river channels are represented on the map, with other permanent water-bodies not represented, but presumably inhabited by adults. Note the sparse densities of adults associated with the main Okavango Channel.

3.4.3 Correction Factors

I. Spotlight surveys

Spotlight surveys detected 22.4 % of all crocodiles present in the low-water season (September – February), and 13.3 % of all crocodiles present in the high-water season (March – August). The annual mean number of crocodiles estimated by means of the mark-recapture study (n = 2 621 animals) was used as a total population size (Chapter 2). Thus, correction factors were calculated by dividing the CMR population estimate by the seasonal spotlight survey population estimates. The correction factors were 7.49 (low-water season) and 4.46 (high-water season) respectively (Table 13).

Table 13. Spotlight counts compared with mark-recapture estimates for all size classes of crocodiles combined, with resultant correction factors for high- and low- water periods. Crocodiles were more concentrated in the main, accessible channels in the low-water season.

Period	Spotlight counts		Mark-recapture estimate	Spotlight counts	Spotlight correction factor
	Average density	# of crocodiles estimated	# crocodiles estimated	% of animals observed	
low - water (September to January)	1.94	588	2621	22.43	4.46
high - water (February to August)	1.154	350	2621	13.34	7.49

II. Aerial and spotlight surveys

Spotlight surveys counted 13.3 % and 22.4 % of the adults in the high- and low - water periods respectively, and correction factors were therefore 5.0 (low - water) and 7.49 (high - water). The percentage of crocodiles counted during the aerial surveys was therefore 56.7 % (low - water) and 77.7 % (high - water) of the adults estimated from the spotlight counts. Thus, correction factors for the aerial survey were calculated as 1.77 (high - water) and 1.28 (low - water) (Table 14).

Table 14. Spotlight counts (SP) compared with aerial survey estimates, including only adult crocodiles for low- and high-water periods. Low-water periods were between September and February, while high-water periods were from March to August. The average annual population estimate (Chapter 2) from mark-recapture methods (CMR) was used to calculate correction factors (CF) by dividing the CMR estimate by the estimates obtained from the spotlight and aerial surveys. (SP) refers to spotlight surveys.

Season	Average Density (SP)	SP estimate	CMR estimate	Aerial survey estimate	% of animals observed (SP)	SP survey CF	% Obs Aerial	Aerial survey CF
LW	0.442	133.926	670.7	521	19.97	5.0	77.7	1.28
HW	0.296	89.688	670.7	380	13.37	7.5	56.7	1.77

3.5 DISCUSSION.

3.5.1 Spotlight surveys

Within the panhandle region of the Okavango Delta the most significant environmental factor influencing the number of crocodiles encountered was water level. The highest encounter rates, especially for the larger crocodiles, were during the low-water when crocodiles were largely restricted to the main channels and permanent side channels, which were accessible by boat. Hutton & Woolhouse (1989) found water level alone to account for 61 % of the variation in the proportion of the crocodile population seen during spotlight surveys in Lake Ngezi, Zimbabwe. Thus, for the purposes of determining long-term population trends, the low - water period would be the optimal time period to conduct spotlight surveys. In the panhandle, the average encounter rate of crocodiles observed over the period of this study was 1.19 crocodiles.km^{-1} ± 0.11 animals. Combrink *et al*., (in Press) reported an encounter rate of 0.38 crocodiles.km^{-1} in Lake Sibaya, South Africa, while Leslie (1997) reported a density of 4.7 crocodiles.km^{-1} in Lake St. Lucia, South Africa. Unfortunately, neither of these surveys reflects sustained, long term counts, and may have been misleading in terms of actual densities in the systems. In the Zambezi River below the Kafue River confluence, an average encounter rate of 3.99 crocodiles.km^{-1} ± 2.61 was reported for 14 spotlight surveys conducted between September 1987 and November 2003. Again, these surveys were sporadic and general correction factors were applied to obtain corrected density estimates.

I. Correction factors

The panhandle data showed that the proportion of the crocodile population encountered differed significantly between seasons, with 22.4 % of the population being encountered during low - water periods compared with 13.3 % of the population encountered during high - water periods. Correction factors for a spotlight survey by Bayliss *et al*. (1986) for three different habitat types [wide (100 m) river with few bends, 50 % vegetation cover; narrow (50 m) with many sharp bends, 80 % vegetation cover; very narrow (10-20 m) with many sharp bends, 100 % vegetation cover] revealed that 66 %, 59 % and 35 % respectively of all crocodiles present were detected by spotlight.

II. Spotlight survey correction factors

Due to the fact that spotlight surveys for crocodiles do not sample all individuals, leading to errors in estimates of abundance, correction factors were used to correct for these biases. In a

study by Brown *et al*. (2004), spotlight counts were undertaken for the stretch of the Okavango River within the Caprivi Strip of Namibia. The above study most probably far underestimated the Nile crocodile population in this area, as a correction factor of 2.22, based on *C. porosus* census data (Caughley, 1977), was used. Using the same correction factors on the spotlight data obtained during the course of the panhandle study, these estimates would have doubled or quadrupled our population estimates. The current study showed in this instance that correction factors should not be based on different populations or different species.

As mentioned above, Hutton and Woolhouse (1989) found that if spotlight counts were undertaken only during the low-water period, most of the variation in the Ngezi counts would have been accounted for and uncorrected counts would probably have provided useful indices of abundance. In the case of the panhandle, this may not be the case (without correction factors). Within the entire panhandle system, main and side channels were lined by thick stands of *Phragmites* and Papyrus (*Cyperus spp.*). This contributed to the decreased detection of individuals, especially in the high - water season, when crocodiles were able to swim amongst this vegetation and therefore away from the boat-accessible channels. The main channel of the Okavango River was between 50 and 80 m wide, whereas channel width decreases to approximately 10 m in the side channels, with many bends leading to differential visibility biases that were not calculated. Season-specific correction factors would be recommended for future studies due to the large difference in detection rates between high and low - water periods.

III. “Eyes only” observations

The increase in the proportion of eyes only observations towards the end of 2006 may reflect an increase in wariness of animals due to learning over the four year study period. This tendency was apparent for some of the study sites during a study on *Melanosuchus niger* and *Caiman crocodilus* in Equador (Ron *et al*., 1998). The number of eyes only observations correlated with the density of panhandle adults and subadults and to a lesser extent juveniles, suggesting that these size classes were becoming more wary with time when compared to the smaller size classes. It is well documented that larger crocodilians are more wary (Webb & Messel, 1979; Hutton & Woolhouse, 1989; Woodward & Moore, 1993; Ron *et al.*, 1998) and therefore more difficult to approach. This study showed that larger animals learnt to avoid perceived and repeated threats at a faster rate than smaller animals. The recapture rate for smaller animals in the panhandle tended to be significantly higher than that for larger animals, emphasising this point.

Crocodiles in the northern panhandle took advantage of the many shallow sandbanks when water levels rose, resulting in the strong correlation between increasing water level and eyes only observations as they were often some distance from the boat and unapproachable.

The lack of hatchlings and subadults in the panhandle is a source of major concern. Letnic and Connors (2006) found that *C. porosus* populations were dominated by these size classes in areas associated with nesting in the Northern Territory, Australia, (see also Messel *et al*., 1981). These were populations that had recovered from over-utilization. Crocodile ranchers remove an annual quota of 2000 eggs (8 000 eggs over the last 4 years). In 2006 this quota represented over half of the total number of clutches in the panhandle, and all of the clutches in the northern panhandle. It is possible that, without the replacement of breeding animals through the release of juveniles that originated from wild eggs, the panhandle crocodile population will not be able to recover from past utilization, or sustain itself in the near future (Bishop *et al.*, in Press).

3.5.2 Aerial surveys

The high densities of mature animals recorded in the Kgala Thaoga area and fairly high densities over the Phillipa and Moremi channels were consistent with the number of nests found in these areas (Chapter 4). While higher densities in the northern Panhandle were unexpected due to high human disturbance in the area, it was noted that the majority of these crocodiles were not sighted along the main Okavango River channel, but instead along the Kgala Thaoga channel and in the surrounding floodplains where access was difficult for people. With the onset of the breeding season, adults were expected to congregate in favoured nesting areas. The surveys confirmed our a priori expectations that these animals utilised the floodplains during the high-water periods, only returning to the main channels when receding water forced them to and only if permanent water was not found anywhere else.

In an aerial survey carried out in Cuba it was estimated that 88 % of crocodiles were not detected from the air (Ramos *et al.*, 1994). Crocodiles are aquatic, cryptic species and therefore animals less than 2 m in total length are not easily visible from the air (Norton-Griffiths, 1978). This problem is exacerbated by dirty or turbid water, the presence of vegetation, or reflection of the sun off the waters' surface (Jacobsen, 1991; Games, 1994; Combrink, 2004). However, the timing of our surveys ensured that crocodiles were basking, and were therefore easily visible from the air. In addition to this, very low densities of adults were observed, thus increasing the likelihood of accuracy (Norton-Griffiths, 1978). The type of aircraft used is an important factor with regards to the percentage of animals seen. Helicopters provide slow cruising speeds, safe

low-altitude flying and the ability to manoeuvre with twisting rivers and streams when counting crocodiles (Pooley, 1982). Helicopters also have the ability to hover when a group of animals is seen so that they can be counted and they offer a wider field of view than fixed-wing aeroplanes. However, despite this, helicopters are very expensive to run and maintain. High survey speed can cause an observer to miss animals, whereas low speeds can lead to double-counting of animals at high densities (Combrink, 2004).

In the southern Pantanal, a large seasonal floodplain showing marked seasonal weather and water level differences, ultralight counts showed a marked difference in densities of caiman counted (Coutinho & Campos, 1996). The low - water, warm and dry winter period yielded markedly higher densities of Caiman than did the high - water (also warm) periods (4.3 ind.km^2 and 147 ind.km^2 respectively). An ultralight has the advantage over other, larger fixed-wing aircraft by being able to fly safely at much lower altitudes and at much lower speeds, thus giving observers more time to observe individuals. The disadvantages of using ultralights for surveys include not being able to carry more than one passenger, which limits the accuracy of the counts due to the inability of the researcher to be able to correct for observer bias. This problem could probably be overcome by using video-based survey techniques.

I. Aerial survey correction factors

The number of animals that are missed while in the observers' field of view determines how accurate counts will be. A method of correcting for observer bias, the "tandem count method" has been used in crocodilian surveys for population and nest counts (Magnusson *et al*., 1978a; Bayliss *et al*., 1986). In retrospect, having an idea of the difference between the "wet" and "dry" season counts, a tandem-count approach can be useful, at least initially in each survey, to calculate the degree of observer bias.

II. Water level effects on density

In the Pantanal, as in the panhandle system, water level was the most important factor affecting caiman density (Coutinho & Campos, 1996). Rising water levels prompted caiman to disperse throughout the very rich and productive, newly flooded areas. This effect was much more marked for individuals in rivers than those frequenting permanent lake areas, with lower seasonal variation. Another important factor affecting adult densities may be reproductive cues, causing them to aggregate in the onset of the breeding season. The effect of water level on encounter rates is not a new observation (Woodward & Marion, 1978; Messel *et al.*, 1981;

Wood *et al.*, 1985; Webb *et al.*, 1990; Ron *et al.*, 1998). Messel *et al*. (1981) found that large crocodiles that were sighted were not necessarily sighted again at low tide. Wood *et al*. (1985) found that *Alligator mississippiensis* also dispersed during high - water seasons. Where the floodplain was narrow, with little adjacent wetland, densities were not significantly correlated with water level. While this scenario holds for the far northern reaches of the panhandle, from the border to Shakawe, the floodplain increases in width downstream. However, this may have accounted for the lack of correlation between water level and densities recorded in the northern panhandle. In addition, large areas of former floodplain in the northern panhandle have been converted to grazing areas, and there is a great deal more human traffic in this region than in the southern panhandle. Human activities were suggested as a reason for a lack of correlation between density and measured "natural" variables in Florida's *A. mississippiensis* populations (Wood *et al*., 1985).

3.5.3 Spotlight vs aerial counts.

Aerial counts in a survey of Caiman conducted using an ultralight (Coutinho & Campos, 1996) correlated significantly to spotlight counts in the same region. Bayliss *et al.*, (1986) mention that spotlight surveys (per km) in Australia cost up to four times as much as helicopter surveys and so spotlight surveys are the cheaper option for assessing whether the total population is increasing, decreasing or stable (Webb, Pers. comm., 2007). However, aerial surveys require a great deal more "observer" calibration than spotlight surveys, and without calibration variation in annual counts must be expected to be highly variable and less precise (Webb, Pers. comm., 2007). However, in an African context, spotlight surveys are far cheaper than aerial surveys.

The success of both spotlight and aerial surveys in the panhandle system depended on timing. More accuracy was obtained when surveys were conducted in the low-water season, between September and February. This ensured that the crocodiles were confined to accessible areas for spotlight surveys. During aerial surveys, water level played a major role in the observer's ability to count animals. This study showed that aerial survey methods conducted during the low - water season provided a much more sensitive measure of adult abundance than spotlight survey methods. This was also noted for helicopter counts in Australia (Webb & Messel, 1979; Ron *et al*., 1998), and was said to be due to an adult's tendency to be more wary of spotlights than the smaller size classes. To maximise efficiency, aerial and spotlight surveys in the panhandle should be conducted in the low - water season.

3.6 CONCLUSION

The rigid structuring of future surveys, with particular emphasis on the timing and placement of transects within the panhandle, and concurrent calculation of correction factors for observer bias, would provide the basis for spotlight count estimates, enabling accurate trend analyses within the panhandle population (see Woodward & Moore, 1993).

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CHAPTER 4:

THE BREEDING ECOLOGY OF THE NILE CROCODILE (*CROCODYLUS NILOTICUS*) IN THE OKAVANGO DELTA, BOTSWANA AND THE IMPACT OF HUMAN-RELATED DISTURBANCE.

4.1 ABSTRACT

Four Nile crocodile nesting surveys were conducted by boat and on foot in the panhandle region of the Okavango Delta from 2002 - 2006. An annual average of 50 nests (49 - 54) was located between the Botswana / Namibia border and 20 km south of Seronga village. The number of nests not found was probably not more than 10 % based on the amount of suitable habitat. The total number of nests located represents a 50 - 60 % decrease in the number of nests that were active 20 years ago. Human induced disturbance levels were highest in the north-western panhandle, associated with high population densities. These disturbance levels were reduced to the south-east as channels become less accessible, the floodplain became wider, and human densities were lower. In the more disturbed areas, breeding females showed a tendency to situate their nests further from accessible channels and in more hidden locations. There was a lack of nests in those areas along the main channel immediately adjacent to settlements.

4.2 INTRODUCTION

Throughout the twentieth century the Nile crocodile (*Crocodylus niloticus*) population of the Okavango Delta, Botswana, has been subject to the ever-increasing impact of human-related disturbance. Between 1957 and 1988 this population underwent three major periods of human-induced decline, resulting in the permanent removal of 12 000 - 50 000 adults and at least 14 000 eggs from predominantly the panhandle region (Pooley, 1982a; Graham *et al.*, 1992). In 1988 the total population of Nile crocodiles in the Okavango Delta was estimated to be approximately 10 000 adults (Simbotwe, 1988)[14]. Subsequently a further nine adult crocodiles (three males and six females) and approximately 8000 eggs were collected in this region from 2003-2006 for the stocking of a crocodile ranch.

Nile crocodiles are oviparous, pulse breeders and nest in summer at the end of the dry season, when sandbanks are exposed and daily temperatures are at their highest (Cott, 1961; Blomberg, 1976; Pooley, 1982b; Kofron, 1990). Wild female crocodilians reproduce every two to three years, while dominant males reproduce annually (Graham, 1968; Kofron, 1989; Lance, 1989). In Southern Africa, the nesting season and incubation is between September and February (Pooley, 1982b; Hartley, 1990; Kofron, 1990). Larger females tend to lay more eggs per clutch that are on average larger than those of smaller breeding females (Pooley & Gans, 1976). Sexual maturity is reached by females over a fairly large size-range and is locality and resource dependant. In the Okavango, crocodiles reach sexual maturity at 2320 mm TL (Detoeuf-Boulade, 2006). Nests are constructed in a range of substrates, from clay to course-grain, pebbled river sand, and the female lays between 40 and 80 eggs in a chamber which is excavated for this purpose[15] (Pooley, 1982b). The eggs lie between 100 - 300 mm below the surface (Kofron, 1989; Grenard, 1991) and the cavity is shaped to suit the substrate (Kofron, 1989). Once the eggs have been deposited in the nest chamber they are covered with sand and incubated by the sun for approximately 90 days (Cott, 1961; Graham, 1968; Pooley, 1969; Blomberg, 1976). Active nest sites are associated with permanent fresh water, which the females require to escape danger and to thermoregulate while guarding the nest (Pooley, 1982b). As such, the majority of nests are within 20 m of permanent water, and may be as far as 100 m away, although this is unusual (Kofron, 1989; Graham *et al.*, 1992).

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[14] Population estimates were assessed through the use of aerial surveys taken along the course of the Okavango river system in 1988.

[15] The number of eggs in a clutch ranges considerably, dependent on the length of the female and availability of resources. The average clutch size from Lake Kariba, Zimbabwe is 45. Blake, D.K. & Loveridge, J.P. (1975). The Role of Commercial Crocodile Farming in Crocodile Conservation. *Biological Conservation*, **8**, 261-272., but ranges from 20-90 (Departmental records, Department of National Parks and Wildlife Management, Harare - cited in Games, 1990)

Female Nile crocodiles guard their eggs for the duration of incubation (Pooley, 1969; Hutton, 1984; Thorbjarnarson, 1992) and for up to six weeks after hatching, often not feeding during this period.[16] Breeding therefore represents a large physiological investment in mature breeding females. Defence of the nest may become aggressive when the nest site is approached too closely, and as Pooley (1982b) described it "succeeds in putting a human intruder to flight". However, this is not always the case and females may abandon nests when disturbed by human intruders (Kofron, 1989). Abandoned nests are routinely predated by many species, including primarily the Water monitor, *Varanus niloticus*, which may be responsible for predation of up to 50 % of nests (Pooley, 1982b; Kofron, 1989; Trutnau & Sommerland, 2006). In Australia, approximately 25 % of *C. porosus* eggs usually hatch in the wild due to predation and flooding (Webb & Manolis, 1993).

Along with several other reptile species, crocodilians exhibit temperature-dependent sex determination where the sex of the hatchlings is determined by the average temperature around the clutch in the second month of incubation i.e. there are no sex chromosomes. This has potentially large-scale effects on population sex-ratios. Leslie (1997) discovered that an alien plant, *Chromolaena*, had invaded the nesting regions in Lake St. Lucia, Kwazulu-Natal, and this was shading the nests, causing a predominance of females hatchlings. Over the past 100 years, global warming has increased by an unprecedented 0.6 ^{0}C, and is projected to continue to rise at a rapid rate (Root *et al.*, 2003). In a study of 143 species of animals, more than 80 % that showed changes were shifting in the direction expected on the basis of the known physiological constraints of the species (Root *et al.*, 2003). The rate of increase of global temperature far exceeds the ability of crocodiles to physiologically adapt to change, or to track these changes, leading directly to female-biased populations at first, followed by extinction in a worse-case scenario. The incubation temperature of the clutch does not only affect gender. It also affects the probability that embryos will survive to hatching, growth rates before and after hatching, and the probability of hatchlings surviving to two years of age (Hutton, 1987; Webb & Cooper-Preston, 1989). The selective advantage of TSD is that it assigns maleness to embryos with high probabilities of surviving and good potential for post-hatching growth (Webb & Cooper-Preston, 1989). Males are produced from clutches in the Okavango panhandle when the average incubation temperature in the middle trimester is between 31.4 ^{0}C and 33.4 ^{0}C (Maciejewski, 2006).

[16] This investment in time and energy may be the reason that wild females do not breed every year, whereas farmed animals do.

No scientific research has been conducted on the Nile crocodile population in the Okavango Delta for over 15 years, and at present the status and recruitment of the population is unknown. Population vital statistics (survivorship, fecundity, growth rates and age [size-class] structure) must be quantified for the sound management of commercially exploited species or the impacts of management strategies cannot be predicted (Kay, 2004a, b). The primary goal of this study was to assess the current breeding status of the Okavango Nile crocodile population in the panhandle region of the Okavango Delta, assessing present and potential future sources of disturbance.

4.3 MATERIALS AND METHODS

4.3.1 Study site

Located within the Republic of Botswana, the Okavango Delta (Figure 23) is the world's largest inland Delta and is also the world's largest RAMSAR site.[6] The Okavango River, which feeds the Delta, is shared by three countries—Namibia, Angola, Botswana—and has a total catchment area of more than 111 250 km^2 (Mendelsohn & el Obeid, 2004). Upon entering Botswana via Namibia, the Okavango River forms a floodplain commonly known as the panhandle. The Okavango River is channelled for the first 107 km from the Botswana/Namibia border by a set of parallel fault lines (McCarthy, 2004) and is known as the panhandle (Figure 24). The Okavango River eventually fans out from the panhandle to create the Okavango Delta, an alluvial fan of immense, annually flooded wetlands bordered by the Kalahari Desert. The Okavango Delta covers an area of approximately 16 000 km^2 in the dry season and over 22 000 km^2 in the annual flooding season (Mendelsohn & el Obeid, 2004).

Figure 23. The location of Botswana and the panhandle region of the Okavango Delta, Botswana, in which this study was undertaken.

[6] The Ramsar Convention is the Convention on Wetlands of International Importance.

This study was conducted in the panhandle region as historical data suggests that 99 % of crocodile breeding, and therefore recruitment into the crocodile population of the Okavango Delta occurs in this region (Graham *et al.*, 1992).

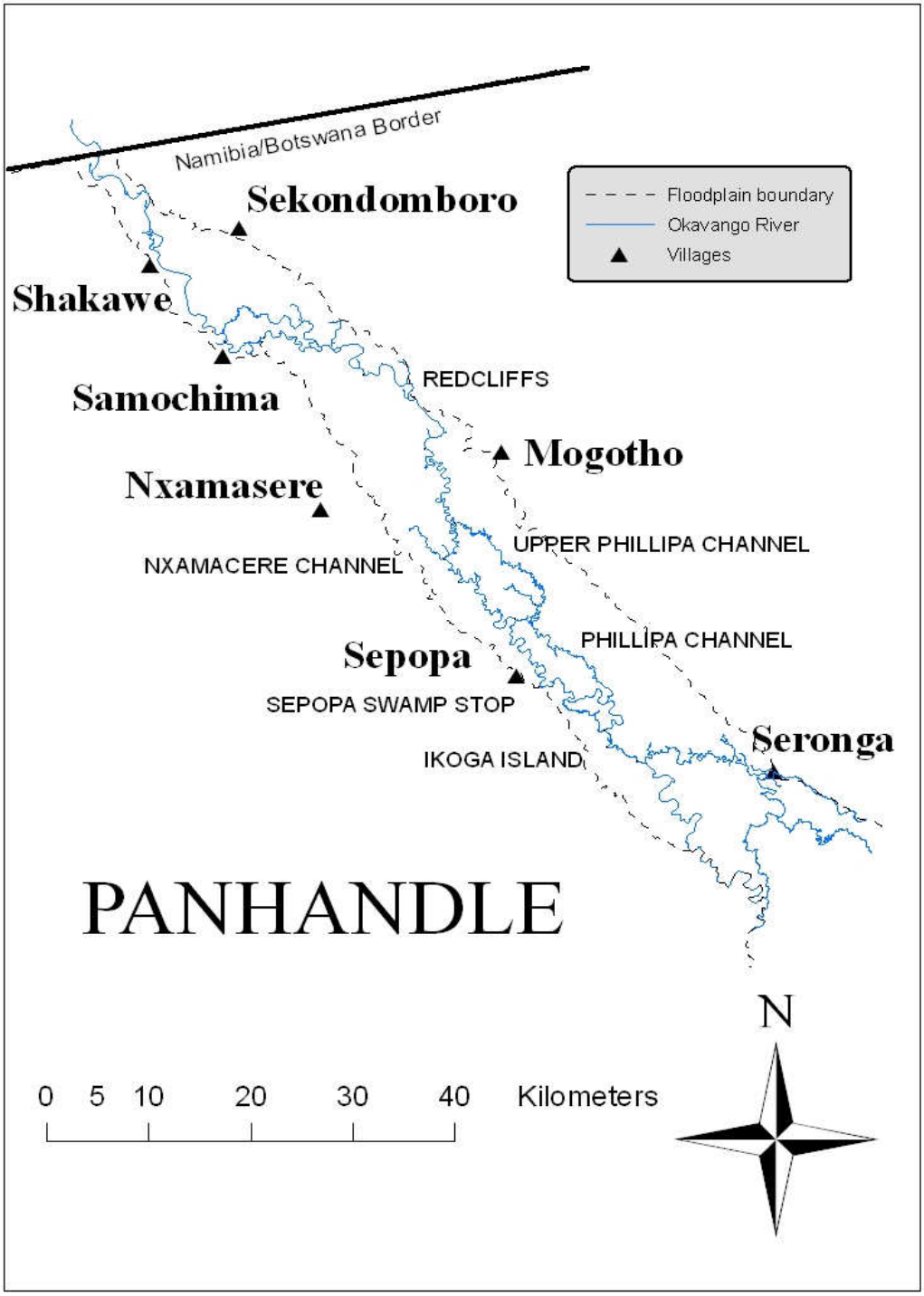

Figure 24. The panhandle region of the Okavango Delta, Botswana, within which the study was undertaken.

4.3.2 Study animal

The Nile crocodile *(Crocodylus niloticus*) is among the best known biologically of all crocodilian species and occurs in 42 African countries, of which approximately 20 populations have been scientifically assessed, the results of which are outlined in Thorbjarnarson (1992) and Ross (1998). Crocodilians exist throughout the tropics, and are considered "keystone" species that maintain ecosystem structure and function (Thorbjarnarson, 1992). A keystone species has a disproportionate effect on its environment relative to its abundance, and removal or decline of that species from the ecosystem will have a dramatic effect in maintaining ecosystem structure and function. In the case of crocodiles, this may include selective predation on fish species (Cott, 1961; Pooley, 1982b), recycling of nutrients, and maintenance of wet refugia in droughts (Thorbjarnarson, 1992; Ross, 1998).

Crocodiles' life histories are categorized by slow development, long life and delayed and repeated reproduction, where the risk of reproductive failure is minimized by repeated breeding rather than by maximizing output (Tucker, 1995). They are long-lived animals with high mortality rates in the first year after hatching due to predation (Woodward *et al.*, 1987). Crocodilians are often the largest predators in their aquatic environments, with terrestrial mammals including humans and livestock falling victim to them. Many species worldwide are exploited for their skins, and many populations are threatened due to hunting for trade (Glastra, 1983; Mourao *et al.*, 1996; Thorbjarnarson & Velasco, 1999; Thorbjarnarson *et al.*, 2000; Santiapillai & Silva, 2001). In addition to this, populations worldwide are threatened by habitat loss, pollution and over-harvesting (Thorbjarnarson, 1992).

4.3.3 Breeding habitat availability in the panhandle

Shacks (2006) undertook a study on the breeding requirements of adult female *C. niloticus* within the panhandle region of the Okavango Delta, and the impacts of disturbance on these breeding females regarding nest-site selection. He showed that 68 % of the total area of the panhandle region fitted the habitat criteria profile on which breeding females were basing their selection of nesting-sites (Figure 25).

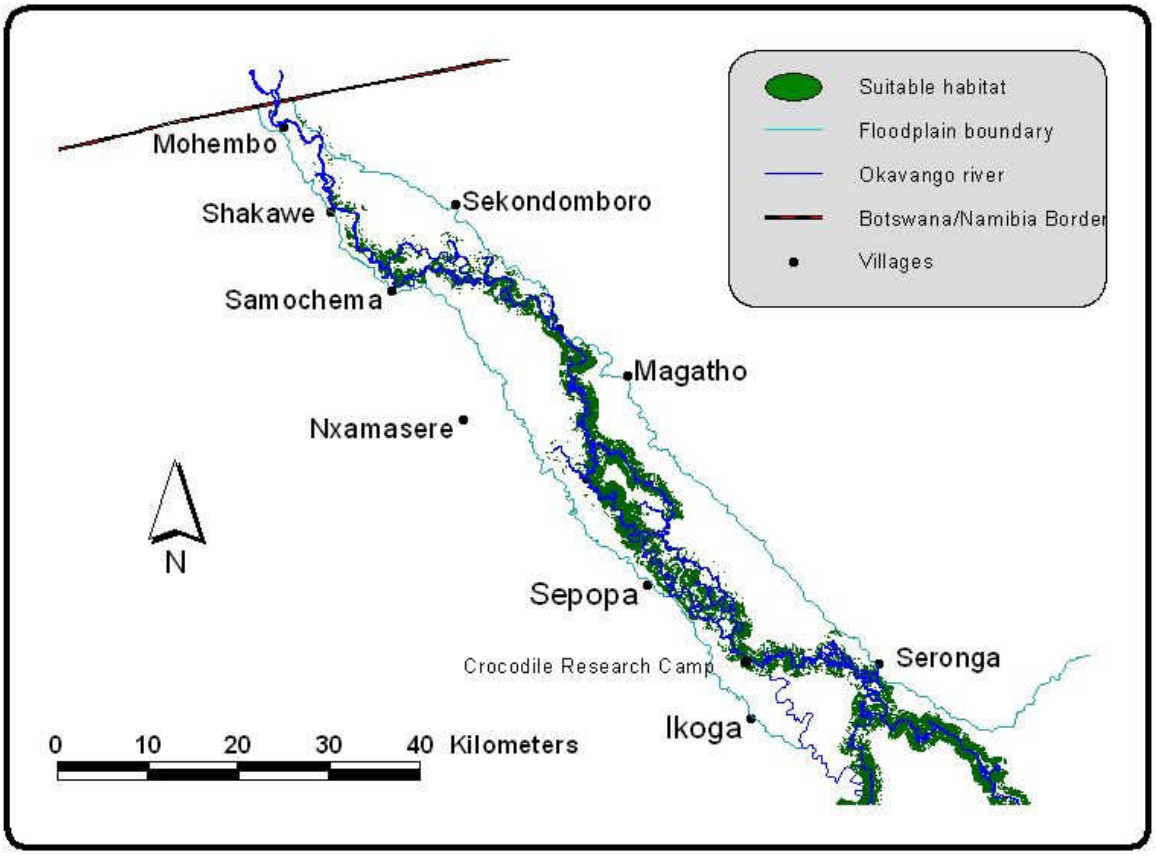

Figure 25. The area in which nesting habitat is suitable for breeding females The majority of the panhandle region (68 %) that was in close proximity to permanent water was suitable for nesting (Shacks, 2006).

4.3.4 Nesting surveys

Nesting surveys were conducted from September to October for four consecutive breeding seasons from 2002 to 2006. The survey area covered the length of the Okavango River from its point of entry into Botswana at its northern border with the Caprivi Strip of Namibia, to Seronga village in the southern region of the Okavango Panhandle (Figure 24).

Historical data suggested that nesting densities were highest in the north-western panhandle, as high as 1 nest.km^{-1} and decreasing to 0.1 nests.km^{-1} in the region of Seronga village (Graham *et al.*, 1992). An experienced local guide was hired to assist with the surveys and all potential sites identified using a series of aerial photos covering the entire panhandle region were visited, including all sites known to the guide, who was employed by crocodile ranchers to collect eggs for them over the past 30 years.

Within the Okavango system Nile crocodiles are unevenly distributed, although the majority of the breeding animals, and 99 % of the nests, are found in the panhandle region where permanent water provides a more stable environment than the Delta region (Graham *et al.*, 1992). Access to the nesting areas was gained by means of a 5.8 m aluminium flat-bottomed boat powered by a 60 hp Mariner outboard motor. After approaching potential nesting sites as close as possible from the main channels of the river, the team proceeded on foot to the sites to assess and record current nesting activity at each location. Nesting localities were recorded using a GPS and subsequently mapped using ArcGIS 9 (ESRI, 2006). The panhandle was divided into 5 distinct zones for the analyses (Figure 26).

The 2003 / 2004 nesting season was the only season in the duration of this study in which the nests of the panhandle were left undisturbed by ranchers. The fates of these nests were therefore determined during a post-hatching survey by careful observation in and around the nesting site in February 2004. Clutches were recorded as “hatched” if the nest had been excavated by the attending female, and if the eggshells had an "exploded" appearance, where the top of the egg had been forced open by the emerging hatchling. Predated nests were often surrounded by scattered portions of eggshells bearing tooth-marks, normally attributed to the primary egg-predator in the region, *Varanus niloticus*, or with the remains of embryos. Flooded nests contained the entire submerged clutch of eggs, and abandoned nests were recorded where there was no recent evidence of an attendant female crocodile, i.e. no body imprint or with vegetation covering the nest. Nests that were made inaccessible due to the presence of an attendant female were recorded as hatched, and those that were inaccessible due to rising flood waters were recorded as “inaccessible”.

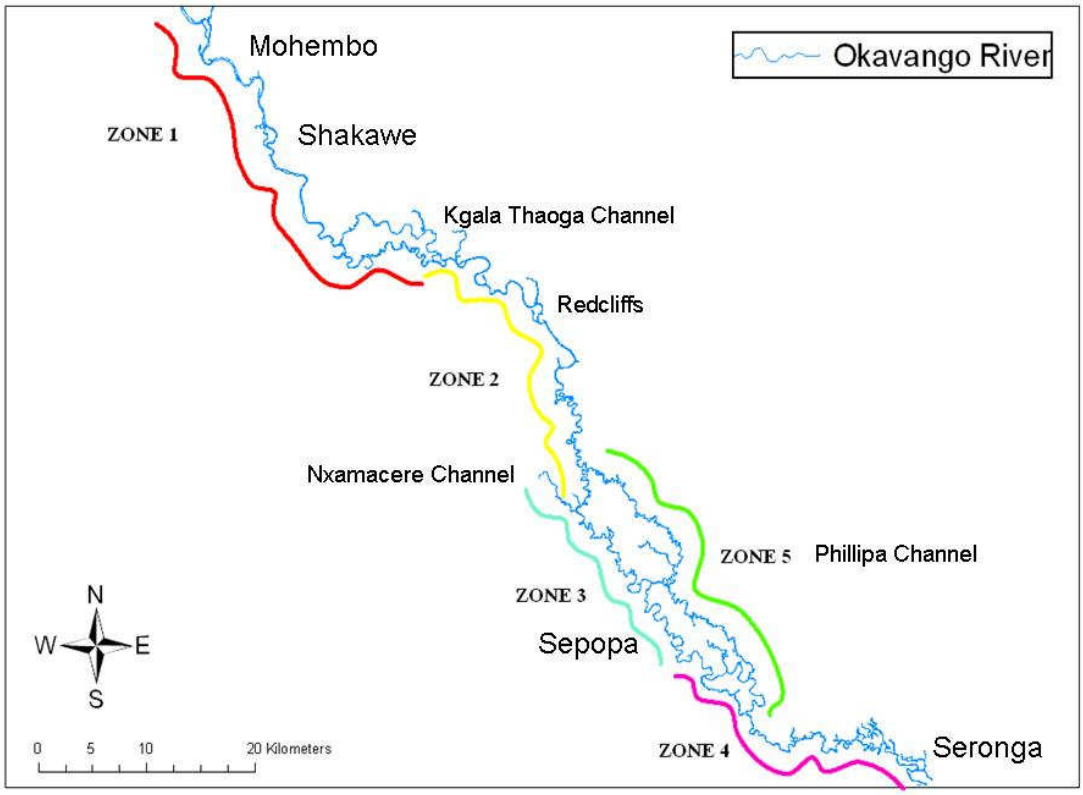

Figure 26. River zones along which nesting surveys were conducted by the Okavango Crocodile Research Group from 2002 - 2006. These zones were based on those of Graham *et al.*, (1992), and the surveys and density analyses were conducted separately for each zone. The zones are as follows:

Zone 1: Shakawe / Kgala Thaoga

Zone 2: Kgala Thaoga / Nxamacere

Zone 3: Nxamacere / Sepopa

Zone 4: Sepopa / Seronga

Zone 5: Phillipa

4.3.5 Spatial analysis

A spatial analysis was performed using ArcGIS v. 9 (ESRI, 2006). In this analysis nest locations for each year were plotted, and the distances to the nearest main villages bordering the panhandle floodplain (Shacks, 2006), were determined. The distance of each nest sight to the nearest accessible deep-water channel (i.e. that the research team could gain access to by boat, thereby indicating general accessibility to humans and potential levels of disturbance) was measured to assess whether or not breeding females were preferentially selecting nesting sites away from potential areas of disturbance. In addition, the distance of each nest to the nearest village

(irrespective of size) and the distance of each village from the nearest access point to the river were measured. In the case of Seronga village, this distance was to the main channel, as Seronga lagoon acts as a disturbance buffer to the main river channel, and most villagers utilize the lagoon for their river-based resources. A basic index of disturbance was then calculated by dividing the population (CSO, 2001) (www.cso.gov.bw/census/dist70_71_72_73.html, accessed 20 September 2007) of each village by its distance from the river. Thus, a large village that was situated close to the river would have a higher disturbance index than a small village situated further from the river. Pearson's product-moment correlations (Zar, 1974) were then performed to investigate the relationships between each variable and north / south co-ordinates were included in this analysis. This analysis was confirmed using a non-parametric Spearman's rank order correlation.

4.3.6 Nest effort

The average nest-effort, or proportion of adult females that are in breeding condition that actually nest was calculated for the period 2002-2006, firstly by using Chabreck's (1966) formula, and secondly by using data collected on the average annual number of mature females producing elevated levels of plasma vitellogenin from mid-July to early September (Detoeuf-Boulade, 2006) i.e. the number of females in breeding condition in the panhandle.

Nest effort (*E*) was calculated from the formula (Chabreck, 1966; Leslie, 1997)

$$P = \left(\frac{\mathrm{N}}{\mathrm{A}^{*}\mathrm{F}^{*}\mathrm{E}} \right) {}^{*}100$$

modified to solve for

$$E = \left(\frac{P/100N}{A^{*}F} \right),$$

where *E* is nest effort, or the proportion of the adult female population that is breeding, *N* is the number of nests, *A* is the estimated proportion of the total population, including both males and females, capable of breeding based on their size (mature), *F* is the proportion of mature females in the population and *P* is the estimated total population size (Bayliss, 1987; Leslie, 1997) (Table 15).

Nest effort was then calculated using the proportion of adult females in breeding condition

(60 %) as determined by Detoeuf-Boulade (2006), the average annual number of nests from 2002-2006 (n = 50), and the number of adult females (n = 364) calculated using Bayesian techniques (Chapter 2).

Table 15. Estimates and explanations for the calculation of nest effort for the panhandle crocodiles

	Estimate	Explanation
F	55.6	Proportion of females in the adult population; obtained using spotlight count data (Chapter 2, Chapter 3)
N	50.0	Number of nests per annum located during nesting surveys (2002 - 2006)
P	2621	Estimated annual population size, estimated using Bayesian capture-mark-recapture methods and spotlight count methods (Chapter 2, Chapter 3)
A	25.3	Annual average proportion of adults, obtained using spotlight count methods (Chapter 2, Chapter 3)

4.3.7 Nest site characteristics

At each nest-site, a number of characteristics were recorded in 2003/2004 and 2004/2005 seasons as part of another study (Shacks, 2006). These were:

1. Date and nest number
2. Positional data was recorded with a Magellan 315 GPS as UTM co-ordinates, Cape datum
3. Substrate/habitat: A general description of dominant ground-cover (sand, vegetation type) was obtained through visual inspection of the area surrounding each nest site
4. The distance to the nearest permanent water was measured using a standard flexible tape-measure (m). Shacks (2006) reported the average distance to water as 137 m, with a maximum distance of 919 m. This was the distance to the nearest deep water channel, not the distance to the nearest permanent water, which may have been a permanent hippo channel or minor stream leading into surrounding floodplains.
5. Each nest's height above water was measured using a standard flexible tape-measure (m)
6. The amount of direct sunlight received by each nest was estimated as the percentage of direct sunlight on the nest per day.

7. Depth to first egg: The depth to the upper-most egg was measured in centimetres, using a straightened length of eight-gauge wire. The bottom end of the wire was rounded to reduce chances of egg damage. The probe was inserted into the soil above the egg chamber to the point of resistance from the top egg. This depth was then measured (cm).
8. The snout-vent length (SVL) of nesting females was measured where possible. The body-print of the breeding female was often visible in the nesting substrate. The SVL was measured in centimetres from the tip of the snout to the cloacal opening, marked by an indentation or a wet area created by the female urinating while lying on the nest. These data were compared to data collected previously by other authors (Cott, 1961; Graham, 1968; Hutton, 1984; Kofron, 1989; Games *et al.*, 1992; Swanepoel, 1999; Botha, 2005).
9. Other comments:

   These included evidence of predators, utilisation of site by humans (waste, fire ash, etc.) and any other notable features.

4.4 RESULTS

4.4.1 Nesting surveys

In the 2002 / 2003 season, a total of 50 nests were located in the panhandle region. Egg collecting for the Krokavango crocodile farm began in the 2004 / 2005 breeding season and continued annually with a quota of 2000 eggs per year, to be taken from the northern panhandle. The 2003 / 2004 season produced a total of 54 nests, including "ranched" nests, the fates of which were recorded. The 2004 / 2005 season produced 49 nests (including "ranched" nests) and the 2005 / 2006 season, 50 nests (including "ranched" nests) [Appendix 2].

Post-hatching visual inspection of 39 of the 54 nests recorded in the 2003 / 2004 season (15 of 54 nests were inaccessible during this period due to rising floodwaters), 21 clutches successfully hatched, 15 were predated, two were flooded and one was abandoned and did not hatch (Figure 27). No nests were recorded between Shakawe village and the Namibia /Botswana border in the 2003 / 2004 season. Zone 1 had 12 nests. There were eight nest sites known to the guide further along the Kgala Thaoga channel that could not be reached due to blockages in the river channel and these sites were not investigated for active nests. These blockages, caused by rising water levels that carried and lodged drifting Papyrus rafts into narrow stretches of channels, were commonly encountered. Of the 12 active nests that were located in the 2003 / 2004 season, four of these nests hatched, four were predated, probably by *V. niloticus*, and four were inaccessible. Most of these nests were situated in isolated locations along hippo channels, away from the main channel. Only 17 of the 25 nests found in Zone 2 were accessible due to rising floodwaters. Eight of these nests hatched, two were flooded and seven were predated by *V. niloticus*. Both Zones 3 and 4, a stretch of 80 km of river, yielded only three nests; one was abandoned by the female and did not hatch, one was predated by a *V. niloticus*, and one nest became inaccessible due to flooding. There were 14 nests in Zone 5. Nine of these nests hatched, three were predated and two were inaccessible due to rising floodwaters. The Upper and Lower Phillipa channels, also known as the "Eastern Channel" is a remote side channel. The nests along these channels were located close to the channels (within 20 m), indicating the relative security of nesting there.

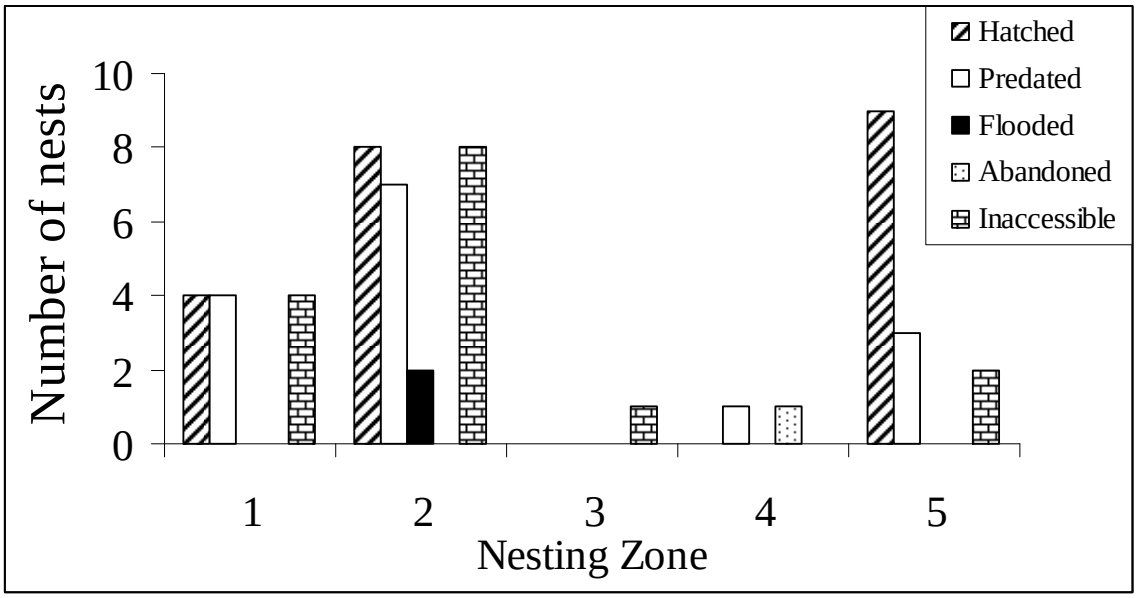

Figure 27. Fates of individual crocodile nests for the 2003 / 2004 nesting season. A total of 54 nests are represented. The nesting sites were visited post-hatching and the fate of the clutch determined by visual inspection of the cavity and its surroundings.

In the 2004 / 2005 season, a total of 49 nests were recorded. Fourteen nests in the Phillipa channel were used for research purposes in the 2004 / 2005 season. Temperature recorders (tidbits) were placed in these nests to record incubation temperatures (Maciejewski, 2006). The fates of these nests were therefore not regarded as natural, and were not used in this analysis.

In the 2005 / 2006 season, a total of 50 nests were located. The Krokovango crocodile farm harvested 36 of these clutches (72 % of all nests found in the panhandle) for incubation and commercial use from the northern panhandle, of which 5 % of the number of eggs collected were to be released as healthy juveniles back into the wild. Of the remaining 14 nests, nine hatched, one was infertile and four were predated. The zones along the western side of the main Okavango river channel (Zone 3 and 4), offered relatively easy access to local fishermen and reed-cutters from Nxamacere and Sepopa villages, and therefore showed very low nest densities in general (< 0.05 nests.km^{-1}, Figure 28). This was particularly the case in the nesting season, when water levels were low (Mbaiwa, 2002; Shacks, 2006).

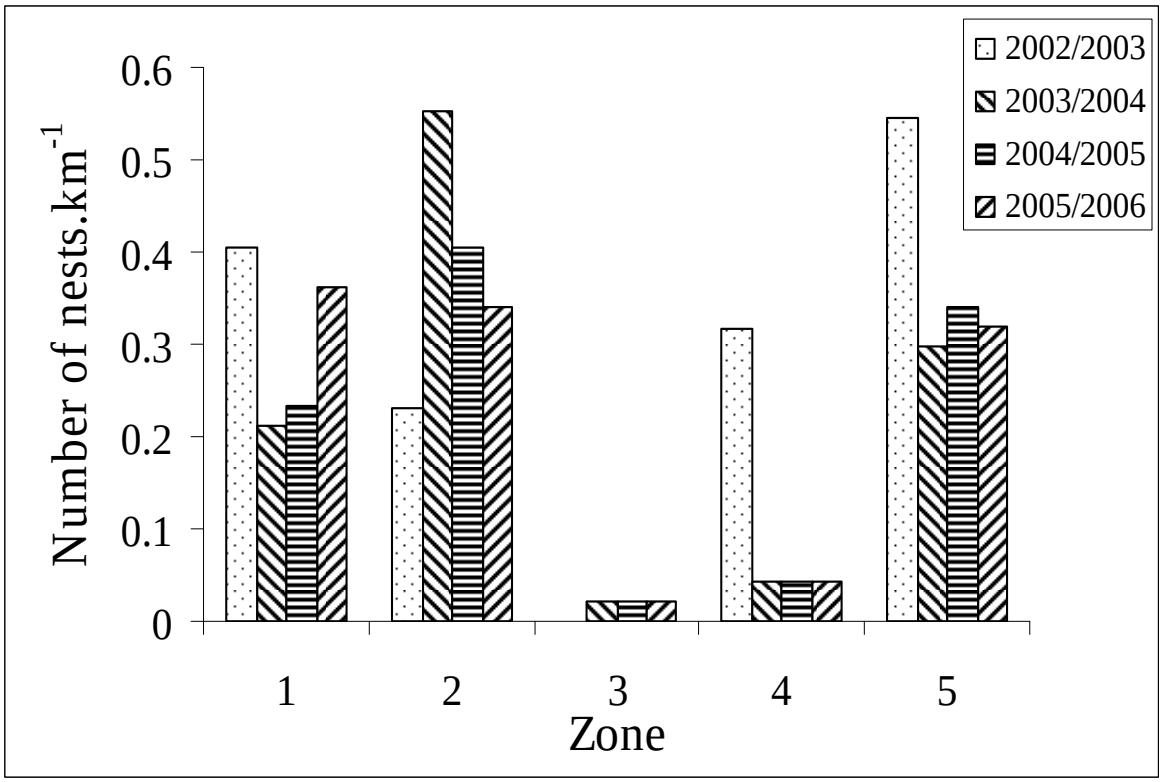

Figure 28. The annual nest densities per zone for the panhandle region of the Okavango Delta for the nesting seasons from 2002-2006. X - axis categories explained in Figure 26.

The nests found along the main channel were, on average, located further from the river than those along the back channels. Along the Okavango River channel itself, nests were situated further from the river in the northern Shakawe area, and the further south and east the nests were located, the closer they were to the main, accessible channels.

The majority of active nest sites located in the 2002/2003 season were used more than once by nesting females in the four consecutive years during which this study was underway (Figure 29). Only 36 % of nest sites were used once, while 42 % were used twice, although not necessarily consecutively, 13 % were used three times and 9 % were used four times. It was not determined whether females exhibited nest site fidelity or whether females were nesting annually.

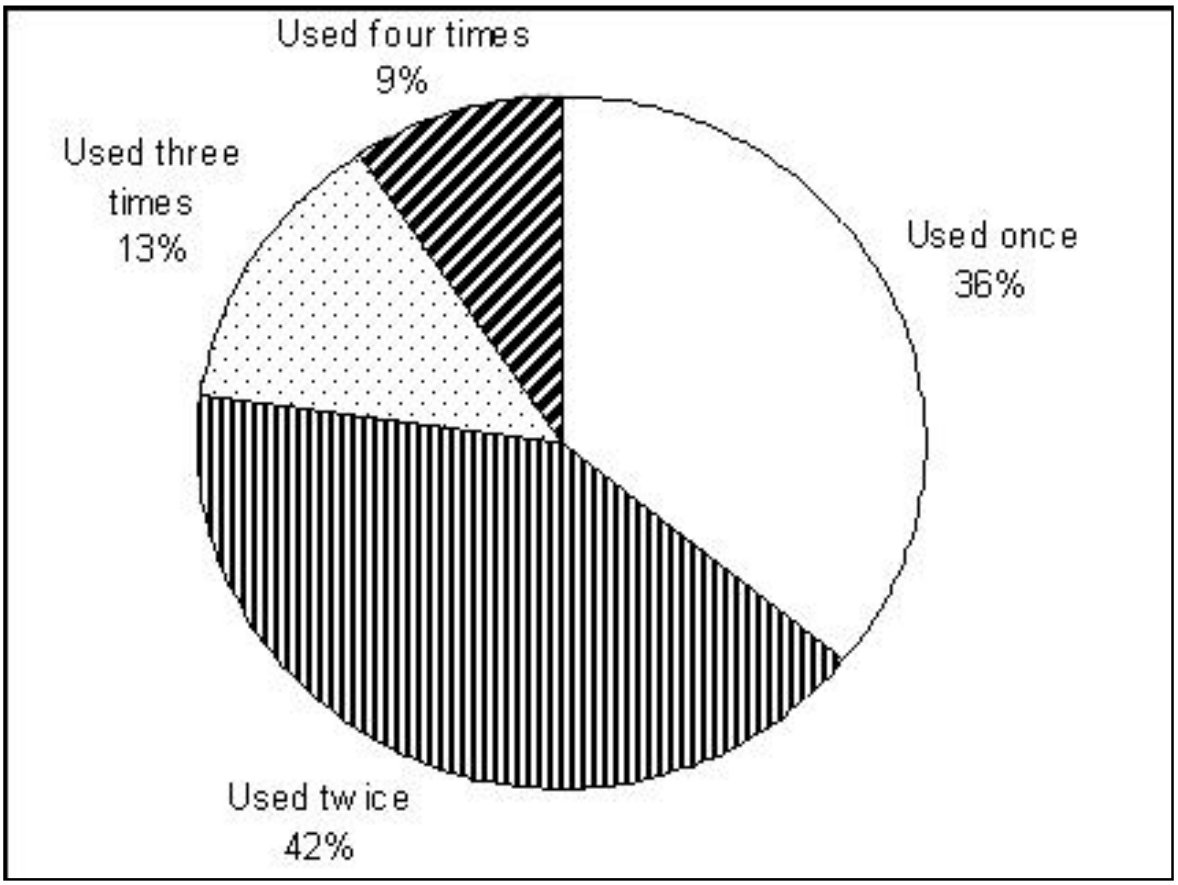

Figure 29. Nest site utilisation from 2002 - 2006, showing the proportion of all active nest sites used once, two times, three times and four times. These sites were not necessarily used in consecutive years, and may indicate that females were not breeding every year.

4.4.2 Spatial analysis

I. Disturbance index

A disturbance index was calculated by dividing the 2001 population of each main village bordering the panhandle region, by its distance from the river (Table 16). A number of general trends were found with regards to the location of the nest sites. The disturbance index was closely correlated to both coordinate variables, with the level of disturbance decreasing significantly (Pearson's product-moment correlation, $p > 0.05$, Appendix 1) to the south and east of the panhandle. In conjunction with this, the further south and east the nests were located, the closer they were located to accessible channels (Appendix 1). However, the disturbance index did not significantly correlate to the distance of nests from the river (Pearson's product-moment correlation, $p > 0.05$, Appendix 1).

Table 16. The main villages in the panhandle region, their localities, populations and calculated disturbance indices (the population divided by the distance from the river)

Village	UTM E	UTM N	Population (2001)	Distance to River (m)	Disturbance Index
Mohembo	581881	7979752	2306	402	5.73
Ngarange	601153	7971040	1987	4611	0.43
Shakawe	588097	7970452	7874	788	10.00
Nxamasere	604791	7945371	1466	8879	0.17
Sepopa	623966	7928333	2308	1750	1.32
Seronga	649191	7918551	3043	830	3.67
Ikoga	634999	7914482	1414	5046	0.28

4.4.3 Nest effort

After solving Chabreck's (1966) equation, an annual nest effort of 14 % was obtained. However, using the data from Detoeuf-Boulade (2006), a nest effort of 22.9 % was calculated for the panhandle crocodiles.

4.4.4 Nest site characteristics

Nesting females require permanent water close to their nests to thermoregulate while maintaining vigilance over their nest. The average distance that crocodile nests were located from permanent water in the 2003 / 2004 season was 7.7 m ± 5.8, with the furthest nest located 30 m from the nearest water-body. This nest was located along a hippo channel that ran some distance from the main channel, in a fairly inaccessible area of floodplain. The female was observed returning to the hippo channel along a well-worn hippo path. The remoteness of the location may have allowed her to nest at this distance from water. To incubate successfully, egg chambers must be located above the water table, where gas exchange can still take place. In the panhandle (2003 / 2004 nesting season), the bottom of the egg chambers were 500 - 2200 mm above the river water level. This was determined by subtracting the depth of the nesting cavity, measured post-hatching, from the height of the top of the nest above water. The average depth of the nest cavities was 496 mm, and ranged from 400 – 640 mm (Maciejewski, 2006). The average height above water at the top of the nests was 1300 mm ± 1100.The uppermost eggs were

located 101 mm ± 66 below the surface, ranging from 50 - 290 mm. For a more detailed description of nest site characteristics see Shacks (2006) and Maciejewski (2006).

In substrates where no body prints were left by attending females, SVL could not be determined. A total of 42 SVL measurements were recorded, and breeding females ranged in SVL from 1400 mm (2740 mm TL) to 2300 mm (4510 mm TL), averaging 1800 ± 212 mm (SD) (3520 mm TL) in length. A total of 12 % of breeding females that left body prints were between 2000 - 3000 mm TL, 62 % were between 3000 - 4000 mm TL, and 26 % were older females between 4000-5000 m TL.

A mixture of sand and grass covered 47 % of the surface around nest sites, followed by sand only (26 %), a combination of sand, grass and *Phragmites* (11 %), sand and *Phragmites* (4 %), and *Phragmites* (2 %). The majority of nests (78 %) received over 70 % of daily available sunlight directly onto the surface above the nest cavity (Figure 30).

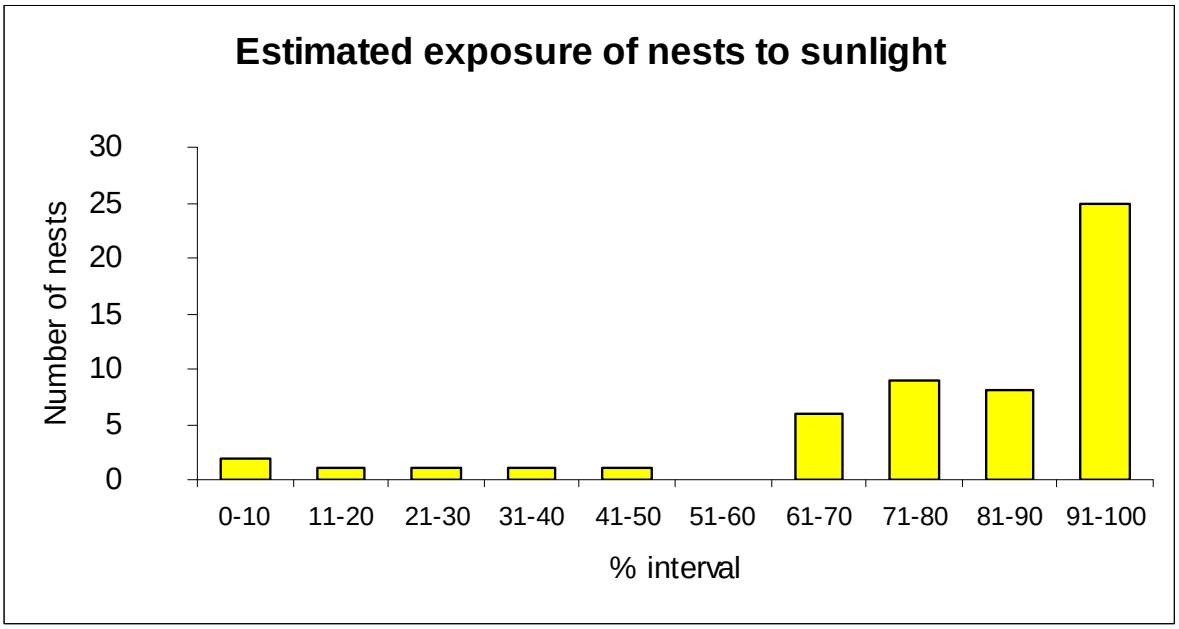

Figure 30. The percentage of total available daily sunlight received by soil surface directly above egg chambers.

4.5 DISCUSSION

4.5.1 Nesting patterns

The patterns of nesting in the panhandle were been fairly stable from 2002 - 2006. Historical data suggests a much larger breeding pool of females up to and including 1987 (Graham *et al.*, 1992). The estimated numbers of nests for those years in which surveys were flown are as follows: 1975 = 105; 1976 = 101; 1978 = 128; 1979 = 135; 1987 = 127. In 1987, 115 nests were identified by farmers who collected 76 clutches and an aerial survey that same year yielded a nest count of 39 additional nests (Graham *et al.*, 1992). There has been a significant decrease in the number of nests over the last 20 years. Current estimates of nest numbers reflect the post-hunting data (Graham *et al.*, 1992) and although official commercial hunting ceased in the 1970's, this activity combined with the collection of mature-length animals for breeding purposes reduced the breeding population in 1987 by 50 % (Graham *et al.* 1992). The nest sites in the panhandle region are not evenly distributed (Shacks, 2006), being associated with deep, active channels (Graham *et al.*, 1992). Areas with high densities of people had few active nests and where present, these nests were likely to be disturbed, thereby potentially reducing the chance of successful hatching.

Under natural conditions, a low percentage of eggs survive through incubation and hatching, with high (30 - 60 %) predation rates, primarily by the Water monitor, *Varanus niloticus (*Blomberg, 1976; Pooley, 1982b; Pers. obs., 2003-2006) or seasonal flooding which drowns embryos. Approximately 2 % of eggs laid actually produce hatchlings that subsequently reach sexual maturity (Pooley, 1982b).

During the low-water season local inhabitants relying on the river's resources, in some cases on a commercial scale, can easily access the floodplains. Crocodiles are feared due to their carnivorous habits (Cassidy, 2003; Thomas, 2006) and are erroneously viewed as competitors for commercial fish species (Cott, 1961; Bruton, 1979). They will on occasion remove fish from nets and damage the nets in the process (Cassidy, 2003). Due to the negative attitude towards crocodiles in the panhandle eggs and nests are destroyed. Although actual numbers are not known, smaller crocodiles become entangled in fishing nets (Pers. obs., 2005), and are likely to become exhausted and drown if not first killed by fishermen.

When flood-waters recede, the floodplains are accessed by herds of cattle that spend the summer months in the Kalahari Sandveld (Murray-Hudson & Parry, 1997). The panhandle floodplain is

legally accessible to cattle-grazing. Although the numbers of cattle in the region is still relatively low (after the slaughtering of ~ 307 000 head to contain a bovine pleuro-pneumonia outbreak in 1996/1997) (Murray-Hudson & Parry, 1997), numbers are increasing once again. There are numerous issues regarding livestock in the floodplains, including alteration of the vegetation types from wetland vegetation to grassland (Shacks, 2006) through trampling and over-grazing (Bruton, 1979; Shacks, 2006). In addition to this, livestock are a source of prey for adult crocodiles in the panhandle (Thomas, 2006) and crocodiles posing a threat to livestock are removed from the system, either through lethal control or by relocation to crocodile ranches (Pers. obs, 2005).

The papyrus beds lining the channels are highly combustible in the low-water season, and are burned every year during the nesting season (NRP, 2001; Shacks, 2006) by people, who have easy access at this time. This activity kills breeding females, destroys eggs, removes vegetation cover and negatively affects nutrient levels in the soil and water (Shacks, 2006). Burning of swamps in which *C. porosus* nest only occurs during very dry years, but it is associated with adult nesting females leaving the area, so that nesting declines in the burnt area for many years and increases in the unburnt areas (Webb, Pers. comm., 2007). Although it is illegal to deliberately start uncontrolled fires in the floodplains since the Herbage Preservation Act of 1978 (Shacks, 2006), fisherman, herdsmen and residents utilizing reeds, papyrus, grasses and water-lily bulbs (Cassidy, 2003) still pursue the practice of annual burning. The intensity of fires depends on the extent of the previous flooding event (Cassidy, 2003).

According to a recent survey in the panhandle (Thomas, 2006), local opinion of crocodiles is very negative, with 76 % of interviewees either fearing or disliking crocodiles. However, very few (around 1 %) of interviewees admitted to having eaten crocodile meat, and most denied that they would harm crocodiles. In the 2004 / 2005 nesting season, a commune of four nests on an island between Shakawe and the Botswana / Namibia border, situated within 100 m of each other, had all eggs unearthed and destroyed by local people.

In the Panhandle, females were not observed to defend their nests as much as reported elsewhere (Pooley, 1982b) and abandoned nests after very little human disturbance. Abandoned clutches may be unable to dig their way out of the nest cavity in the fine-grained substrate of the panhandle (Modha, 1967) and perish within the nest.

The effective population size (N_e) of the panhandle crocodiles has been reduced five-fold within the last ~ 80 years. Parental generation N_e has decreased from ~ 480 individuals to a current

estimate for this generation of ~ 90 individuals (Bishop *et al.*, in Press). This result suggests, theoretically, an increased susceptibility to continuing decline of this population as a function of genetic drift and selection, which results from low population numbers. For this reason, the removal of any mature animals from the system has potentially dire consequences for the population, given the current low recruitment rate (Bishop *et al.*, in Press). The removal of eggs, without the release back into the wild or immigration of new animals also has potentially dire consequences in this system (Bishop *et al.*, in Press). The maintenance of the current rate of recruitment is not enough to ensure the long-term persistence of this population. The population must be increased artificially by reintroduction of wild-originating juveniles into the wild by crocodile ranchers that have removed eggs in the past.

4.5.2 Spatial analysis

Historically, there has been a distinct paucity of crocodiles between the entrance to the Upper Phillipa channel and Redcliffs (Taylor, 1973). This pattern persists to this day (Appendix 2). While this remote region supports few crocodiles, it is distant from areas of high human densities, and the nests in this region (Appendix 2) possibly reflect the necessity for breeding female crocodiles to isolate nests from human intruders. Shacks (2006) illustrated that the majority of the panhandle system (68 %) was suitable for and met the physical requirements of breeding females for successful nesting. Shacks (2006) showed that females were probably selecting nesting sites based on the levels of human disturbance they experienced within the panhandle. Females avoided the main Okavango channel in the immediate vicinity of villages. The disturbance index calculated in this study confirmed the increased levels of disturbance demonstrated by Shacks (2006). The general pattern of females nesting away from the main stream on side channels or, if along the main stream, in isolated locations, was especially evident in the Shakawe area. Breeding females no doubt had to select these areas as Shakawe village is not only situated close to the main Okavango channel (Figure 24) with a large total human population (Table 16), but also that floodplain the in this region is very narrow.

The spatial arrangement of nests within the panhandle has undergone a change since Graham *et al.*, (1992) reported decreasing nest densities from between the Namibia / Botswana border and Shakawe village in the north-west panhandle (1.0 nest.km^{-1}), to Seronga village in the south-east panhandle (0.07 nests.km^{-1}). This was no longer the case during this study, with the region upstream from Shakawe village now supporting a maximum of three to four nests per year, reflecting the increased human impacts in this region (Shacks, 2006). Overall, the maximum current nest densities are only 58 % of the pre-1987 levels, and these only in the 2002 / 2003 nesting season in Zone 5, and in the 2003/2004 nesting season in Zone 2, due in both cases to the

presence of large side channels. The Kgala-Thaoga and Phillipa channels are fairly isolated side-channels that provide breeding females with optimal breeding habitat and are relatively isolated from human activity (Shacks, 2006). Graham *et al.*, (1992) reported that 59.4 % of all the nests found were only accessible from papyrus-choked water indicating that this pattern was evident pre-1987. In the Phillipa channel (Appendix 2) which had a low disturbance index, females nested in more obvious locations along the channel, although it was easily accessible by boat. Shacks (2006) showed that this channel (including the Upper Phillipa, Zone 5) would be a suitable area in which to establish a sanctuary area for breeding crocodiles.

4.5.3 Patterns of nest site use

Although 64 % of nest sites in the 2003 / 2004 season were used more than once during the four years, many optimal, previously used sites were not active, especially in the northern section of the panhandle. It has been shown that female crocodiles will display fidelity to a nesting bank, even when alternative sites are abundant (Mazzotti, 1983; Hutton, 1989; Thorbjarnarson & Hernandez, 1993), and the fact that many sites were inactive may indicate a population well below carrying capacity.

4.5.4 Nest effort

Only 14 - 23 % of females that were in breeding condition (n = 218), with elevated levels of vitellogenin (Detoeuf-Boulade, 2006) were in fact breeding during the course of this study. Spectacled caiman in Venezuela were found to have a nest effort of 0.54 (Thorbjarnarson, 1994), with breeding output directly related to female body size. A typical nest effort for the Nile crocodile was estimated to be between 0.6 and 0.8 (Craig *et al.*, 1992). When compared to other studies, the nest effort for the Okavango *C. niloticus* population (0.14 - 0.23) is very low. Graham (1968) reported a nest effort of 0.88 in Lake Turkana while Hutton (1984) determined a nest effort of 0.63 in Lake Ngezi. A nest effort of 0.9 was reported for the Middle Zambezi system (Games, 1990). The nest effort in the panhandle was similar to that shown in a number of other studies of crocodilians (Lance, 1989; Kofron, 1990; Leslie, 1997) and the low nest effort suggests a physiological response to an external stimulus. Nest effort at Lake St. Lucia fluctuated widely (Blake & Jacobsen, 1992; Leslie, 1997), possibly in response to unpredictable environmental conditions such as drought (Webb & Smith, 1987). The panhandle nest effort was stable for the duration of the study, and the panhandle itself is a fairly stable and predictable environment with fluctuations in annual flood levels presenting the major abiotic hazard to breeding success. The lower nest effort in the panhandle may suggest an inhibiting factor to breeding in the Okavango system. If low rates of breeding were not a response to fluctuating

environmental and resource-based circumstances, as in Lake St. Lucia, then human disturbances were most probably contributing to the low level of nest effort. In the Ndumu Game Reserve (KwaZulu-Natal, South Africa) it was reported that crocodiles did not nest from 1962 -1969, and this was attributed to crocodile hunters, destruction of riverine habitat and increased human population densities (Pooley, 1969). A separate example of crocodiles abandoning nest sites occurred in Ndumu Game Reserve in 1963, when a road was constructed near the southern bank of Inyamiti Lake, an area where females had, up until then, nested annually (Pooley, 1982b). At Lake Sibaya (KwaZulu-Natal, South Africa), the number of nests found dropped from 30 to 12 between 1970 and 1972. Many were communal nests that did not survive due to cattle disturbance, illegal harvesting, predation and rising lake levels (Bruton, 1979). It is clear that areas with high densities of people are usually devoid of breeding crocodiles or, if not, are exploited and have a much reduced chance of survival. Added to this problem is the fact that very few of the eggs actually survive through incubation and hatching, with high (30 - 60 %) predation rates (Pooley, 1982b; Pers. obs., 2003 - 2006), seasonal flooding and cannibalism ensuring that only approximately 2 % of eggs laid produce hatchlings that subsequently reach sexual maturity (Pooley, 1982b).

4.5.5 Nest-site characteristics

Graham *et al*., (1992) reported the mean distance of nests to water (n = 35 nests) in the Okavango as 9.53 m ± 7.64 and the greatest observed distance of 256 nests from the water was 60 m. However, Blomberg (1976) reported the mean distance from water as 17 m (n = 36 nests). Graham *et al*., (1992) suspected this to be a typographical error. Modha (1967) reported a range of nest distances from water from 14 localities around Lake Rudolf as 3.1 - 29.8 m. Swanepoel (1999) reported an average distance (n = 33 nests) to water as 18.9 m ± 2.64, with a range of 2.4 - 52.8 m on the Olifants River in the Kruger National Park, South Africa. At the Flagship Boshielo Dam in Mpumalanga, South Africa, Botha (2005) reported and average distance to water as 11.7 m, ranging from 3 – 25.5 m. Generally the nests in the panhandle, while falling into the ranges reported by other authors, were found slightly closer to permanent water (n = 53, 7.7 m ± 5.8 [SD]). However, in the panhandle the nesting banks often gave way to the floodplains behind them, restricting the distance available for females to move away from the channels adjacent to which they were nesting.

Botha (2005) found that 52 % of the nests that he located received between 6 and 8 hours of sun per day. In this study the majority of the nests received over 70 % of daily available sunlight (i.e. over 8 hours of direct sunlight). This may have reflected the different nature of the habitats or substrate types between the two study sites. Kofron (1989) found that female nest attendance

may affect incubation temperature, with female crocodiles often lying over the nest cavities through the heat of the day, at times when the sand was hot enough to “blister human feet”. In hotter areas or at exposed nest sites, this could be a means to protect the clutch from extremely high temperatures.

4.5.6 Size of breeding females

While sexual maturity was initially reached, based on the production of above-average levels of vitellogenin, at 232 cm total length in female panhandle crocodiles (Detoeuf-Boulade, 2006), the smallest female actually nesting was estimated at 274 cm total length and female nesters ranged to a maximum of 451 cm. Other studies on various Nile crocodile populations in southern Africa report the size at which female crocodiles initially attain sexual maturity as 233.4 cm ± 34.6, with a range of 180 - 287 cm (Cott, 1961; Graham, 1968; Hutton, 1984; Kofron, 1989; Games *et al.*, 1992; Swanepoel, 1999; Botha, 2005). While the smallest nesting female (determined by SVL – body print at the nest site) was consistent with results found in other studies, the average breeder was much larger (60 % were between 300 cm and 400 cm). The discrepancy between size at sexual maturity (determined by the production of vitellogenin –Detoeuf-Boulade, 2006) and the smallest breeding female encountered was an anomaly, but may explain the low nest effort. It is possible that smaller and less experienced females may be postponing their breeding, or that enlarged follicles may increase and decrease (reabsorbed) for a few years before a female can obtain the “social status” to nest (Webb, Pers. comm., 2007). While the reasons for this are unclear it is possible that human disturbance may play a role, given the abundance of available nesting habitat.

4.5.7 The impact of crocodile ranching

In Botswana, Nile crocodiles were transferred from CITES I (Convention of the International Trade of Endangered Species; no trade) to CITES II (restricted trade), in January 1990 (Fergusson *et al.*, 2004) allowing ranching practitioners to utilise wild collected stock. The prerequisites for seeking a transfer from CITES I to CITES II are that the population of the species is no longer considered endangered and that the population’s continued recovery and conservation would benefit from a ranching program. The benefits of crocodile are undisputed. In Australia, *Crocodylus porosus* have been protected since 1971 and the population of wild, non-hatchling crocodiles has increased by 50 % since farming was introduced in 1984. The population increased by 4-5 % per year (Webb & Manolis, 1992; Webb *et al.*, 1994). With strict application and enforcement of appropriate legislation, wild crocodile populations and all those involved (in terms of community employment, improvement of local infrastructure, improved

commercial and subsistence fishing, ecotourism opportunities etc) will benefit from crocodile ranching.

Over the last three years, only one ranching program has utilised the wild panhandle population for ranching activities. As Games *et al.* (1992) pointed out, the panhandle population of crocodiles is sensitive to fairly small perturbations, and the harvesting of breeding-sized animals from the system is not sustainable. A comparison of costs and benefits suggested that the export of live adult crocodiles tends to be economically undesirable for Botswana (Barnes, 1996). Barnes (1996) suggested that crocodile ranches in Botswana were financially capable of providing up to 10 % of collected eggs for restocking, although a 5 % restocking percentage was deemed suitable (Barnes, 1996). Games *et al.* (1992) also recommended harvesting strategies involving the collection of eggs from the wild. Provided that crocodile ranchers release 5 % of all animals originating from wild-collected eggs (which has not yet been done), annual harvesting of all nests lying outside protected “sanctuary areas” should continue. As an incentive for ranching practices to continue, it is suggested that eggs are freely available from the wild to licensed crocodile ranchers. The removal of eggs from the wild, with the return of the prescribed percentage back into the wild, will augment the natural population, and as such benefits the population in the long term (Webb & Manolis, 1993; Webb *et al.*, 1994; P.W.S.N.T., 2005). All animals released into the wild should be tested for (at least) *Salmonella* and crocodile pox.

4.6 CONCLUSION

The harvesting of breeding females should not be permitted in the panhandle region until the crocodile population is considered stable. This should be ascertained using nocturnal spotlight survey techniques and monitoring the number of annual nests in the panhandle to assess population trends. However, the harvesting of eggs would be beneficial for the panhandle crocodile population, provided that 5 % of healthy crocodiles from the egg quota are released back into the wild. The establishment of a breeding sanctuary is suggested in the Phillipa channel area to provide breeding crocodiles with an area of little or no human disturbance.

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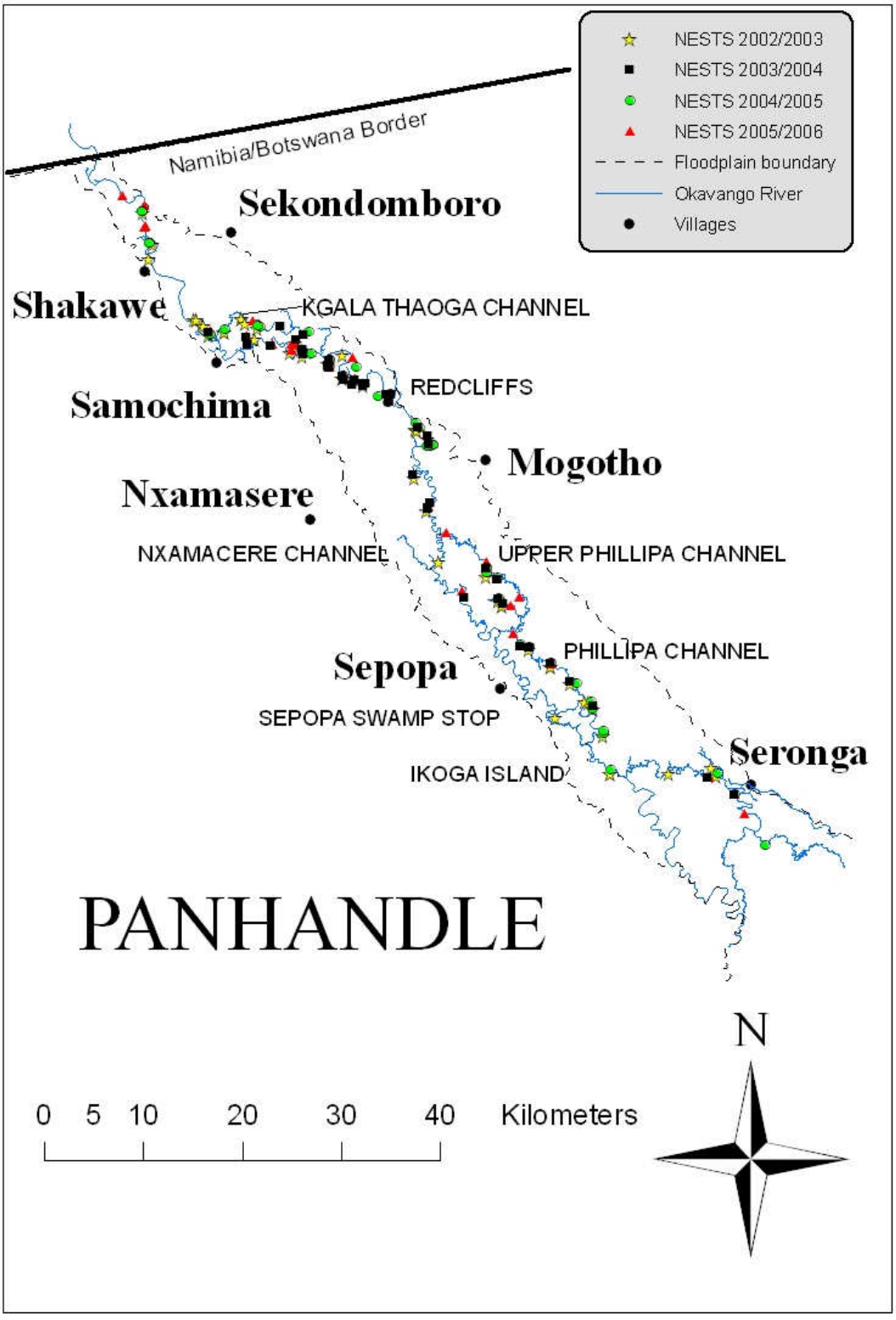
Appendix 1. The results of the Pearson's product-moment correlations. Disturbance decreased to the south and east of the panhandle. Correlations significant at p = 0.05 were emphasised in bold text, and were confirmed by the non-parametric Spearman rank order correlations.

Season		X Coordinate	Y Coordinate	Distance of nest to river (m)	Distance of nest to nearest village (m)	Disturbance index
2002/ 2003	X Coordinate	1.0000	**-0.97**	**-0.29**	0.02	**-0.50**
		p= ---	**p=0.00**	**p=.04**	p=.89	**p=.00**
	Y_ Coordinate	**-0.97**	1.0000	**0.31**	0.12	**0.39**
		p=0.00	p= ---	**p=.03**	p=.40	**p=.01**
	Distance of nest to river (m)	**-0.29**	**0.31**	1.0000	-0.12	-0.21
		p=0.04	**p=0.03**	p= ---	p=0.41	p=0.145
	Distance of nest to nearest village (m)	0.02	0.12	-0.12	1.0000	**-0.43**
		p=0.89	p=.40	p=.41	p= ---	**p=.00**
	Disturbance index	**-0.50**	**0.39**	-0.21	**-0.43**	1.0000
		p=.00	**p=.01**	p=.15	**p=.00**	p= ---
2003/ 2004	X Coordinate	1.00	**-0.96**	**-0.36**	**-0.36**	0.18
		p= ---	**p=0.00**	**p=0.01**	**p=0.01**	p=0.21
	Y Coordinate	**-0.96**	1.0000	0.35	**0.51**	**-0.28**
		p=0.00	p= ---	p=0.01	**p=0.00**	**p=0.04**
	Distance of nest to river (m)	**-0.36**	**0.35**	1.0000	-0.12	-0.02
		p=0.01	**p=0.01**	p= ---	p=0.39	p=0.91
	Distance of nest to nearest village (m)	**-0.36**	**0.51**	-0.12	1.0000	
		p=0.01	**p=0.00**	p=0.389	p= ---	**p=0.00**
	Disturbance index	0.18	**-0.28**	-0.02	**-0.40**	1.0000
		p=0.21	**p=0.043**	p=0.91	**p=0.00**	p= ---

Appendix 1 (cont.). The results of the Pearson's product-moment correlations. Disturbance decreased to the south and east of the panhandle. Correlations significant at p = 0.05 were emphasised in bold text, and were confirmed by the non-parametric Spearman rank order correlations.

Season		X Coordinate	Y Coordinate	Distance of nest to river (m)	Distance of nest to nearest village (m)	Disturbance index
2004/ 2005	X Coordinate	1.0000	**-0.97**	-.2490	-0.04	**-0.49**
		p= ---	**p=0.00**	p=0.084	p=0.795	**p=0.00**
	Y Coordinate	**-0.97**	1.0000	0.33	0.19	**0.37**
		p=0.00	p= ---	p=0.02	p=0.197	**p=0.01**
	Distance of nest to river (m)	-0.25	**0.33**	1.00	0.13	-0.25
		p=0.08	**p=0.02**	p= ---	p=0.37	p=0.09
	Distance of nest to nearest village (m)	-0.04	0.19	0.13	1.0000	**-0.54**
		p=0.8	p=0.20	p=0.37	p= ---	**p=0.00**
	Disturbance index	**-0.49**	**0.37**	-0.25	-0.54	1.00
		p=0.00	**p=0.01**	p=0.09	p=0.00	p= ---
2005/ 2006	X Coordinate	1.0000	**-0.98**	-0.22	0.08	**-0.41**
		p= ---	**p=0.00**	p=0.131	p=0.61	**p=0.00**
	Y Coordinate	**-0.98**	1.0000	0.23	0.01	**0.32**
		p=0.00	p= ---	p=0.10	p=0.97	**p=0.02**
	Distance of nest to river (m)	-0.22	0.23	1.0000	-0.09	-0.15
		p=0.13	p=0.10	p= ---	p=0.53	p=0.27
	Distance of nest to nearest village (m)	0.08	0.01	-0.09	1.0000	**-0.54**
		p=0.61	p=0.96	p=0.53	p= ---	**p=0.00**
	Disturbance index	**-0.41**	**0.32**	-0.15	**-0.54**	1.0000
		p=0.00	**p=0.02**	p=0.29	**p=0.00**	p= ---

Appendix 2. The nest localities for the panhandle region of the Okavango Delta from 2002 - 2006.



CHAPTER 5.

NILE CROCODILE (*CROCODYLUS NILOTICUS*) MORPHOMETRICS AND GROWTH RATES IN THE PANHANDLE REGION OF THE OKAVANGO DELTA, BOTSWANA.

5.1 ABSTRACT

A total of 1717 individual crocodiles ranging from 136 mm - 2780 mm SVL were captured from January 2002 to December 2006 in the panhandle region of the Okavango Delta, Botswana. Overall, 148 (8.6 %) hatchlings, 1018 (59.3 %) yearlings, 311 (18.1 %) juveniles, 177 (10.3 %) subadults and 63 (3.7 %) adults were captured. Inter-capture periods ranged from 1 - 1261 days. A number of individuals were recaptured more than once: 224 crocodiles were recaptured at least once, 44 at least twice, 7 at least three times and one was recaptured five times. Of all the yearlings that were encountered on the river, 81 % were successfully captured and a total of 75 % of recaptures were yearlings. Hatchlings exhibited elongation of the jaw to capture smaller prey items and morphometric shifts in jaw shape coincided with a dietary change at 400 mm SVL. The jaw became broader and deeper as animals matured, in preparation for larger mammalian prey. Adult animals showed morphometric sexual dimorphism, with males and animals in regions with fast-flowing waters having longer tails, probably for more efficient mobility. The average growth rate of recaptured yearlings (170 - 389 mm SVL) was 0.198 ± 0.116 $mm.d^{-1}$ SVL. Growth rate was closely correlated to the amount of time an individual spent in above-average water temperatures. Improved body condition, reflected by increased RCF values, was significantly and positively correlated to a rise in water-level and negatively correlated to time spent in above-average water and air temperatures. Average RCF values were intersected when animals had spent 50 % of their time in above-average temperatures and water level.

5.2 INTRODUCTION

Morphometric relationships allow the prediction of size and condition of crocodilians in the wild and fulfill a basic and practical need arising from research on the ecology of crocodilians (Hutton, 1987b). An animals' physiological state is related to its ability to cope as an individual and has direct consequences in terms of its reproductive success (Jakob *et al.*, 1996). It is therefore possible to calculate a non-intrusive index of nutritional state, or relative "fatness", to provide a snapshot of the individual's physiological state. To do this, one has to separate aspects of body mass that are due to structural size, from aspects that reflect fats and other energy reserves (Green, 2001), thereby controlling for absolute body size. The first of three methods tested by Jakob *et al.*, (1996) is known as the ratio index, ponderal index, or relative condition factor (RCF), where the mass of the individual is divided by a body size indicator (BSI – a linear measure of size). This BSI can be raised to the power of three or, where the slope of the mass/BSI regression does not equal three, must be calculated and assumes that the mass and BSI increase isometrically (Cone, 1989). Although the RCF method (Le Cren, 1951) was designed for and has been used extensively in the fisheries scientific field, it has previously been used for *Crocodylus niloticus* (Games, 1990; Leslie, 1997), *Crocodylus porosus* (Taylor, 1979) and for *Alligator mississippiensis* (Brandt, 1989). The second body condition estimate is the slope-adjusted index, which is similar to the ratio index, but for the calculation of the slope using a (large) independent data set (Jakob *et al.*, 1996). The third index, the residual index, uses the residuals of the body mass / BSI regression, after transformation of the data, to fit a linear regression (normally *ln* transformation). Jakob *et al.*, (1996) recommend using the mass/BSI residual index, as this does not vary with body size, as is the case with the other mentioned indices. However, Green (2001) outlines a number of assumptions when using this method which, when violated, leads to a type I error, where the hypothesis has been rejected when it was true, or a type II error, when the hypothesis failed to be rejected when a given alternative hypothesis was true (Zar, 1974).

In general, *r* values are high in reptiles (Forsman & Lindell, 1991; Weatherhead & Brown, 1996; Dı´az-Paniagua *et al.*, 1997), suggesting that residual indices generated by the least-squares ordinal method are more likely to be reliable for reptiles than for birds and mammals (Green, 2001).

The correlation between crocodilian age and size may be one of the most fundamental life history traits (Webb & Smith, 1987), because it allows age, maturity and senescence to be estimated. However, in large ectotherms, demographic parameters are poorly related to age and

growth is a primary interest as life-history phenomena are related to body size (Peters, 1983; Hutton, 1987a). Reptilian growth rates are typically very variable (Cott, 1961; Blake & Loveridge, 1975; Webb *et al.*, 1978; Hutton, 1987c; Kay, 2004b), both between different cohorts within a region and over a broader geographical scale. Growth rate parameters for the particular population under study are therefore required to make local management decisions (Hutton, 1987c; Wilkinson & Rhodes, 1997). Crocodiles are long-lived animals, with Nile crocodiles living for up to a century, under optimal wild conditions (Branch, 1998). Long-term studies are therefore necessary to collect accurate growth rate data on crocodiles. Due to the high cost of equipment and the challenging logistics involved when working in an aquatic environment, there is little available long-term data on crocodilian growth rates in the wild. Captive crocodilians, under optimal pen densities, feeding and temperature conditions, will grow faster than those in the wild (Hutton, 1987c), sometimes doubling "natural" growth rates (Chabreck & Joanen, 1979). It is difficult to assign ages to wild cohorts after only 3 - 4 years of growth (Cott, 1961; Webb *et al.*, 1983; Hutton, 1984). Different size classes also exhibit differing growth rates, with the growth rate to size relationship changing at 4 - 5 years of age (Hutton *et al.*, 1987). Webb *et al*., (1978) found that a linear growth pattern was exhibited for *C. porosus* up to 800 mm snout-vent length (SVL), but that this fitted line did not describe the growth rates for larger animals. Smaller animals tended to have a much higher relative length-related growth rate than larger animals, whereas larger animals increased at a relatively higher rate in terms of mass.

Graham (1968) attempted to age crocodiles using cross-sections of the ramis of the mandible, the dentary bone and the teeth, indicating seasonal growth spurts. Unfortunately, the success in skeletochronology[17] in this instance was limited due to a number of factors outlined in Hutton (1987c) and only dead crocodiles could be aged (Graham, 1968). However, Hutton (1987c) pioneered a successful aging technique using cross-sections of osteoderms taken from live animals. The most accurate results from this study were obtained from males and non-breeding females, due to the mobilization of minerals (primarily calcium) from non-structural skeletal elements in breeding females for the formation of the egg shells that need approximately 36 grams of calcium per 60 eggs (Hutton, 1984).

Seasonal changes have a significant influence on crocodilian growth. Crocodiles are ectothermic and regulate their body temperature behaviourally, by alternatively sunning themselves to warm up and then moving into water or shade to cool down. Peak basking times occur before and after the midday (Cott, 1961; Modha, 1968). Crocodiles are nocturnally aquatic (Pooley, 1982),

[17] The process in which thickened calcium layers (laminae) are used to calculate the age of the animal.

although may be found ashore moving between habitats or lying on banks on warm, humid evenings (Pooley, 1982). Evenings are spent in the water, where body temperature is buffered from the cooler air temperatures, and this time is used to hunt. Crocodilian growth slows during colder, winter months, and growth rates increase again with increased ambient temperatures (Webb *et al.*, 1983; Brandt, 1989; Games, 1990; Kanui *et al.*, 1991; Zilber *et al.*, 1991; Sah & Stuebing, 1996). Ambient temperature plays an important role in growth (Hutton, 1987a) where sub-optimal temperatures can cause lower feeding and digestion rates. Many juvenile alligators actually "shrink" during the cooler period of the year (Chabreck & Joanen, 1979), decreasing by 1.0 - 4.0 mm in total length per month.

In addition to ambient temperatures, fluctuating water levels have a profound effect on the distribution and behaviour of wild crocodile populations (Pooley, 1982). Seasonal flooding allows crocodiles to exploit new habitats and food sources and this, combined with warm weather, normally results with increased growth rates (Webb *et al.*, 1978; Hutton, 1987a). This is the case in the Okavango panhandle, where annual flooding follows the rainy season and the seasonal floodplains are inundated with water.

The objectives of this portion of the study were to assess various morphometric and growth-rate parameters of the panhandle crocodile population and compare these, where possible, to those of other populations.

5.3 MATERIALS AND METHODS

5.3.1 Study area

The Okavango delta, an alluvial fan (Mendelsohn & el Obeid, 2004) is the worlds' largest Ramsar site[18] and is situated in the North-eastern region of Botswana, Southern Africa (Figure 31). The Okavango Delta is unique in that it is the only delta on earth not flowing into the sea, draining rather into the Kalahari Desert. The Delta has its origins in the Angolan highlands, which provide a catchment area, feeding some 10 000 million m^2 of water into the delta. Local rainfall contributes about half this volume annually (Mendelsohn & el Obeid, 2004). The panhandle region of the Okavango Delta (Figure 32) is approximately 107 km long in a straight line between the Botswana/Namibia border and Seronga and channels the water of the Okavango River until it is discharged into the delta proper. The permanent, swiftly flowing channels are typically walled by papyrus (*Cyperus sp.*) and tall reeds (primarily *Phragmites australis*), with sandbanks on many of the corners along the river's length. Seasonal rainfall in the Angolan catchment (October to February) induces the annual flooding of the delta which extends the wetland area from 16 000 km^2 to 22 000 km^2. The flood water takes approximately six months to reach the southern most areas of the delta due to the very shallow gradient from the north-west to the south-east (Mendelsohn & el Obeid, 2004). This unique area supports an extraordinary diversity of fauna and flora, with approximately 88 native fish species of which 23 are endemic. There have been no introductions of alien fish into the system which in itself is an extremely rare occurrence (Van As, Pers. comm. 2005). The elevated banks and permanent water created by the deposition of sediments make the panhandle the primary breeding region for the Nile crocodile population in the Okavango Delta.

[18] Ramsar – wetland of international importance.

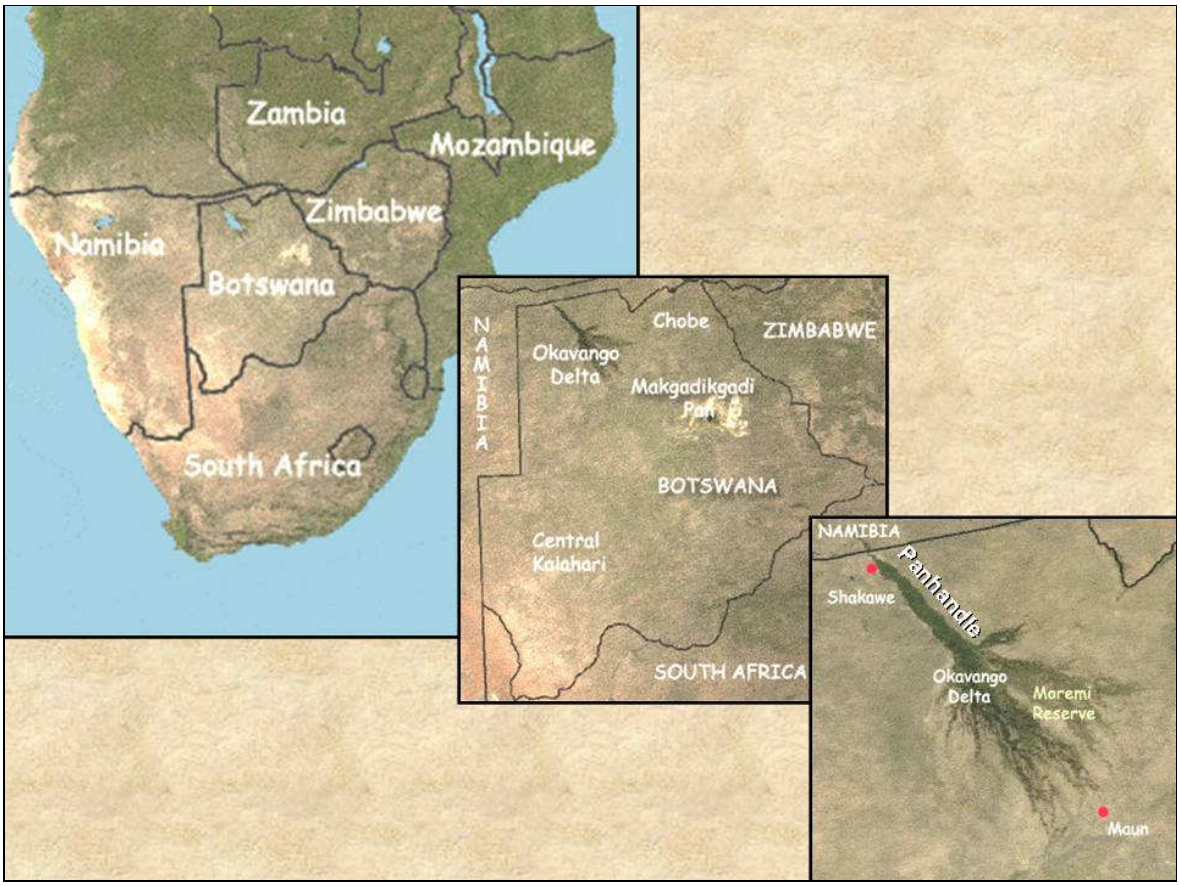


Figure 31. The study area of the Okavango Crocodile Research Group, in the panhandle region of the Okavango Delta, Botswana
(source: **http://www.egnu.com/maps/okavango_map.html**, accessed on 28/07/07).

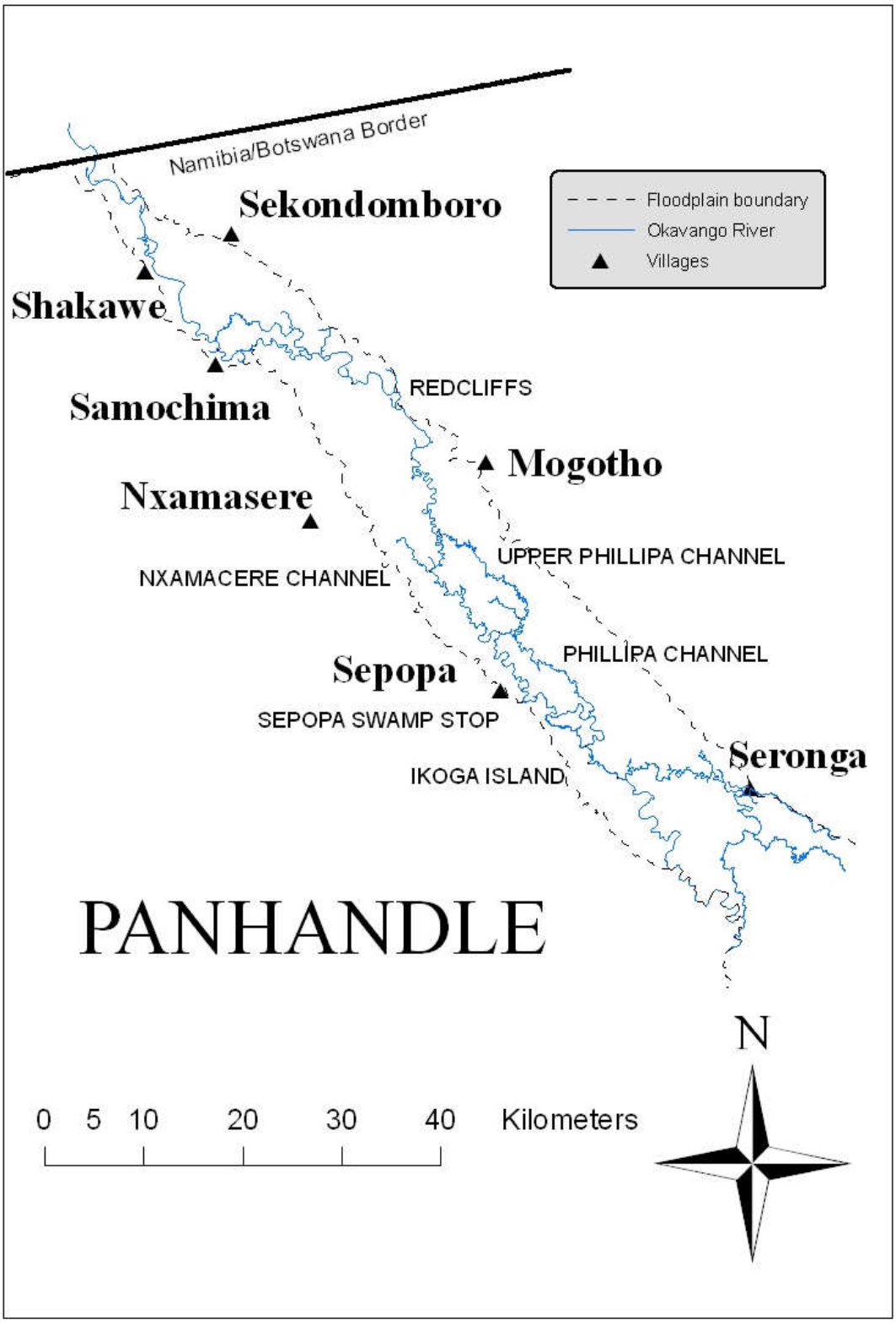


Figure 32. The panhandle region of the Okavango Delta, Botswana, showing the extent of the area in which the study was conducted.

Crocodiles were captured nocturnally using a number of size-dependant capture techniques described in Chapter 2. Once captured and restrained, a number of morphometric measurements were taken and the animals were released within 30 minutes at the site of capture. Morphometric measurements and abbreviations recorded are listed below (Webb *et al.*, 1978; Leslie, 1997):

1. Total length (TL). Tip of snout to tip of tail (0.5 cm)
2. Snout-vent length (SVL). Tip of snout to posterior of first scale row after cloaca (0.5 cm)
3. Neck circumference (NC). Circumference of neck at level of nuchal rosette (0.5 cm)
4. Base of tail circumference (BTC). Circumference of the tail, immediately posterior to cloaca (0.5 cm)
5. Head width (HW). Width of head at level of jaw articulation (0.1 cm)
6. Head depth (HD). Maximum depth of head (0.1 cm)
7. Head length (HL). Tip of snout to median hind edge of supra-occipital bone (0.1 cm)
8. Total body mass (g).

Measurements 1 - 4 were recorded using a standard flexible tape measure. Total length (TL) and snout-vent length (SVL) were measured while the animal was on its back, down the mid-line of the body. Measurements 5 - 8 were made using vernier calipers, sized according to the size of the animals. Animals were weighed using size-dependent Pesola spring scales. Larger crocodiles (> 80 kg) were not weighed due to the logistical difficulties of weighing large animals on a boat. The crocodiles were assigned to classes based on their size, in this case, snout-vent length (SVL), as the tails were damaged in many cases and total length (TL) would often not have been as accurate BSI. The size classes were: hatchlings < 170 mm, yearlings 170 – 389 mm, juveniles 390 – 663 mm, subadults 664 – 1158 mm, adults >1158 mm, following those of Leslie (1997). This was done because it has been demonstrated that crocodiles of different sizes exhibit ecological and behavioural separation (Hutton, 1984; Games, 1990).

5.3.2 Morphometric comparisons

Morphometric measurements were compared between male and female crocodiles from the Okavango region (all size classes), Lake St. Lucia, KwaZulu-Natal, South Africa (Leslie, 1997), Lake Kariba, Zimbabwe (Games, 1990) and Lake Ngezi, Zimbabwe (Hutton, 1987a). These analyses took the form of linear regressions and multiple linear regressions, using sex and location as “dummy” variables. Although HL was used as a standard measure of body length in the past (Webb *et al.*, 1983; Hutton, 1984), the close correlation in this study between SVL and TL (R = 88.1 % - 99.6 %, where animals with damaged tails and obvious errors in recording had been removed) lends confidence to SVL. Therefore SVL was used in the analyses relating to

morphometric relationships as the BSI. The slopes of the regression lines for all size class morphometric measurements were compared using ANCOVA (Zar, 1974).

5.3.3 Growth rates

The daily SVL growth rate ($mm.day^{-1}$) for each crocodile that was recaptured in excess of 120 days after initial capture was calculated to include any seasonal influence there may have been on growth. Growth rates for male and female crocodiles in the panhandle population were tested for differences using ANOVA (Zar, 1974). The growth rates were regressed against mean SVL in the inter-capture period to obtain growth patterns associated with increasing size.

I. Temperature

The average panhandle water temperature was calculated for 2003 - 2005, using temperature data collected at the time of capture of each crocodile during the mark-recapture experiment using a BATT-12 thermocouple meter (Physi-temp, CA, USA) and a Cu – Cn thermocouple probe of 1500 mm in length. The temperature of the water was measures approximately 400 mm below the surface, at the side of the boat. Average monthly temperatures, measured between the hours of 22h00 and 02h00, were used to standardise the water temperature for the duration of the project. A sinusoidal curve was fitted to the water temperature data on a time-series scale (days since January 1, 2003) in the following form:

$$Yt = m + nt\left(A\cos\omega t + B\sin\omega t\right)$$

Where:

$$\omega = 2\pi f$$

The average number of days into the year when water temperature decreased below mean and once again rose above mean was calculated. The proportion of time spent in the “above average” water temperature period between capture and recapture was calculated for all crocodiles caught more than once.

II. Water level

Water level data were obtained from the Department of Water Affairs, Gaborone who recorded daily water levels (in meters) at Stations 7134 (Sepopa) and 7112 (Mohembo).The average monthly water level was calculated from these data and the proportion of time each crocodile spent in above-average water level between capture and recapture was calculated and explored, by means of linear regression analyses, for correlation to growth rates (Webb *et al.*, 1978).

A residual analysis removed the seasonal influence on growth rate so that the influence of size on growth rate could be determined. All analyses were carried out using STATISTICA (data analysis software system), version 7.1. (ESRI, 2006).

5.3.4 Body condition indices

The residual index was calculated using *ln* transformed mass and SVL measurements regressed against each other, using the following equation:

$$LN(mass) = \beta_0 + \beta_1 * \ln(svl) + \delta$$

where β_0 *and* β_1 are constants and δ is a random variable with median 0. The index of body condition is δ , the residual value (Jakob *et al.*, 1996; Schulte-Hostedde *et al.*, 2005).

The ratio index, or relative condition factor (RCF), was calculated using the following equation:

$$RCF = Mass \big/ a * SVL^b$$

where a was the intercept of the regression of the *ln* transformed mass (g) against the *ln* transformed SVL measurement (mm) and *b* was the slope of the regression.

An index using neck and/or tail circumference was also calculated as it is in these areas where crocodilian fat reserves are stored (Games, 1990). This condition index (CI) was first used by Games (1990) for crocodiles from Lake Kariba and the Lower Zambezi River and later by Leslie (1997) according to the following equation:

$$CI = (\frac{CIRC}{SVL}) * 10$$

where "*CIRC*" was the neck or tail-base circumference and "*SVL*" the snout-vent length.

These analyses were conducted separately for sexes, size classes and seasons, as any of these variables may have impacted on RCF (Green, 2001). Each year was divided into two seasons, the period between 15 May - 8 October, when water temperature was below average (non-growth season) and the rest of the year, when water temperature was above average (growth season). These dates were consistent for the time the study was underway.

5.4 RESULTS

5.4.1 Morphometrics

A total of 1717 individual crocodiles were captured between January 2002 and December 2006. Yearlings made up the majority of the individuals, reflecting their natural dominance in the population (Table 17, Chapter 3). Male and female hatchlings were pooled due to the difficulties in sexing hatchlings in the field using non-lethal techniques.

Table 17. Number of individuals captured per size class from 2002 - 2006 from the panhandle region of the Okavango Delta, using nocturnal, boat based techniques and baited traps. Hatchlings could not be sexed reliably in the field using non-lethal methods.

Size class	SVL (mm)	Males	Females	Total
Hatchlings	< 169			185
Yearlings	170-389	537	334	953
Juveniles	390-663	193	122	316
Subadults	664-1158	83	103	186
Adults	> 1158	35	42	77

I. Total length: Snout-vent length relationships

Okavango Crocodiles

Hatchlings increased less rapidly in snout-vent length with increasing total length than the other size classes (Figure 33, Table 18). When hatchlings were removed from the analysis (ANCOVA), the slopes for the other size classes were still significantly different ($p < 0.01$) indicating a significantly higher increase in SVL relative to the increase in TL as animals grew longer. Male and female adults showed significantly different rates of increase and intercepts, with males showing a relatively higher increase of SVL:TL than females. The intercept for females was, however, non-significant ($p < 0.21$, Table 18, Figure 34).

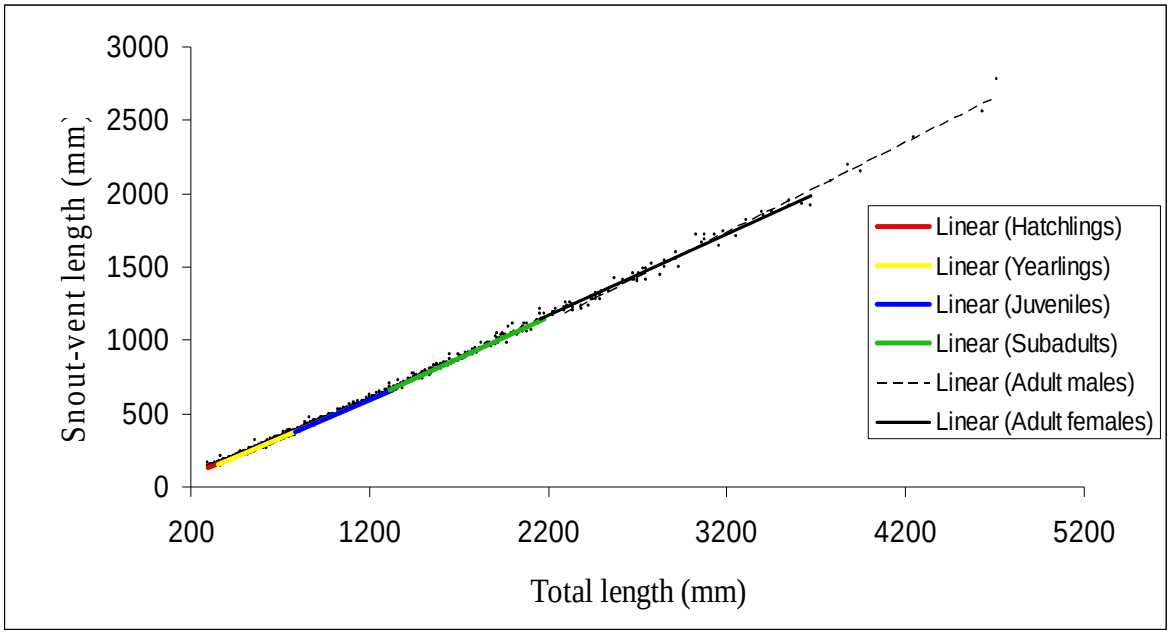


Figure 33. The relationship between SVL and TL of panhandle crocodiles, excluding those crocodiles that had damaged tails, or in cases where data were incorrectly recorded (i.e. obvious outliers). Where two regression lines overlapped in the figure (adult size class), males and females are significantly different at p = 0.01 (n = 1677, Table 18).

When all size classes are pooled, there is a difference between the SVL:TL regression slopes for males (β = 0.552) and females (β = 0.547), with males increasing in tail length at a slightly, but significantly (p > 0.01) faster rate than the females. The 12 largest animals (1875 - 2314 mm SVL = 3455 - 4170 mm TL) were all male, with the exception of one female that measured 1924 mm SVL.

Table 18. Regression results for snout-vent length and total length of panhandle crocodiles. Adult male and female crocodiles were significantly different (p = 0.01), with males growing in SVL at a slightly faster rate than females.

	Slope	SE slope	p slope	Intercept	SE intercept	p intercept	N	SE estimate	r	p estimate
Hatchlings	0.351	0.014	< 0.01	33.49	4.73	< 0.01	185	4.02	0.88	< 0.01
Yearlings	0.51	0.002	< 0.01	-23.56	1.14	< 0.01	937	6.94	0.99	< 0.01
Juveniles	0.525	0.004	< 0.01	-31.90	3.64	< 0.01	306	9.28	0.99	< 0.01
Subadults	0.56	0.005	< 0.01	-71.84	9.08	< 0.01	176	17.09	0.99	< 0.01
Adult males	0.609	0.01	< 0.01	-215.61	31.69	< 0.01	32	39.06	0.99	< 0.01
Adult females	0.556	0.015	< 0.01	-50.55	40.24	0.21	41	38.09	0.99	< 0.21

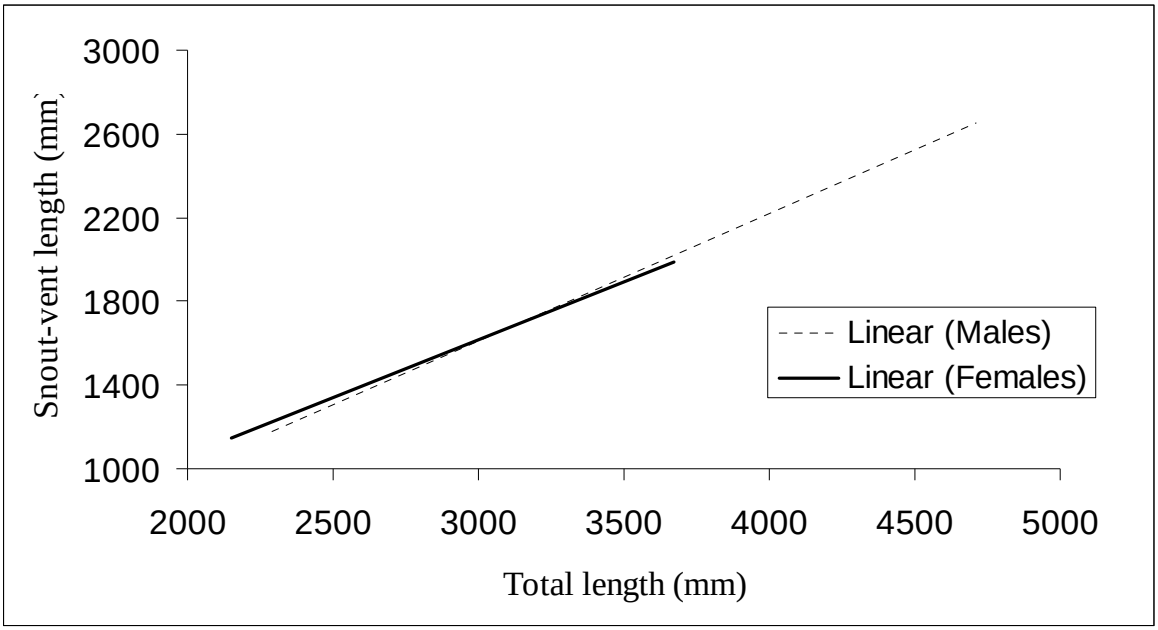


Figure 34. The relationship between panhandle male and female snout-vent length and total length (n = 1677, r = 0.99). Adult male and female crocodiles showed significantly different relationships ($p < 0.01$), with male crocodiles increasing in SVL at a faster rate than females of the same SVL.

Snout-vent length: Total length comparison with the adult St. Lucia and Lake Kariba sub-populations

The St. Lucia adult sample (Leslie, 1997) contained 25 males and 35 females ranging in size from 1150 mm to 2300 mm SVL. The Lake Kariba sub-sample consisted of 26 adults, 10 females and 16 males. These animals were compared with adults from the panhandle, consisting of 31 males and 42 females within the same size range. Where tails were damaged, these data were excluded from the analyses (Table 19). Regression analyses of this subset of data indicated no significant difference between male and female SVL:TL regressions within the St. Lucia sub-sample and within the Lake Kariba sub-samples ($p < 0.01$). There was a significant difference between male and female SVL:TL regressions from the panhandle sample ($p < 0.01$). However, this difference was small and so panhandle males and females were pooled for subsequent analyses. An ANCOVA revealed that there was no significant difference in the slopes ($p = 0.56$) for the three regressions, with a common slope of 1.71 for the three samples. The intercepts were significantly different ($p < 0.01$) from one another and once the common slope was fitted, for any given total length, a St. Lucia adult crocodile had a tail that was 106 mm shorter than a panhandle crocodile and 131 mm shorter than a Lake Kariba crocodile of the same total length.

Games (1990) provided regression results for samples (all size classes) from Lake Kariba (Zimbabwe) and the Lower Zambezi River (Mozambique) and Hutton (1987a) provided equations for the Lake Ngezi (Zimbabwe) crocodiles:

Okavango: TL = 1.82 SVL + 86.60 (SE = 2.78, r = 0.999, p < 0.0001, n = 1676)
Lake Kariba: TL = 1.82 SVL + 93.52 (SE = 9.86, r = 0.99, p < 0.0001, n = 383)
Zambezi River: TL = 1.86 SVL + 36.16 (SE = 16.14, r = 0.98, p < 0.0001, n = 468)

Unfortunately Hutton (1987a) did not publish any morphometric measurements or standard errors for his estimates and so statistical comparisons could not be made with the Lake Ngezi sub-population.

Table 19. A comparison between adult animals (SVL:TL) from the panhandle, Lake Kariba and Lake St. Lucia. The regression values are compared between the three geographically separated populations.

Region	Slope	SE Slope	p Slope	Inter-cept	SE Inter-cept	p Inter-cept	SE Regression	r	n	p Regression
Panhandle (OCRG*, 2007)	1.713	0.03	< 0.01	222.4	46.9	< 0.01	35.6	0.99	73	< 0.01
Lake Kariba (Games, 1990)	1.692	0.04	< 0.01	338.5	80.2	< 0.01	80.8	0.99	26**	< 0.01
St. Lucia (Leslie, 1997)	1.749	0.03	< 0.01	123.1	55.5	0.02	57.4	0.99	58***	< 0.01

* OCRG = Okavango Crocodile Research Group,
** = 2 samples removed due to tail damage
*** = One sample removed due to tail damage.

II. Head length: Snout-vent length relationships

Okavango crocodiles

The panhandle population showed a significant relationship between head length and snout-vent length for all size classes, with HL increasing at a higher rate relative to SVL in smaller animals (Figure 35, Table 20). The slope of the HL:SVL regression decreased step-wise as crocodiles

grew, with adults having the lowest head-length increase relative to SVL. Hatchling head length measurements showed more variation than other size classes and so the intercept for this regression was not significant (Table 20). An ANCOVA confirmed that the regression slopes for the different size classes were significantly different ($p < 0.01$).

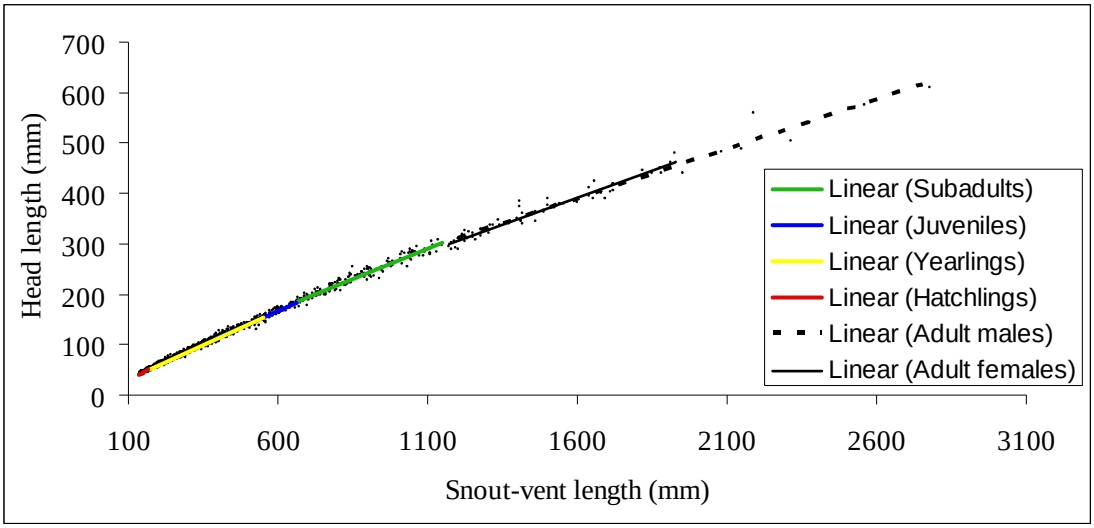


Figure 35. The relationship between head length and snout-vent length of panhandle crocodiles ($n = 1631$, $r = 0.97$). Where trend lines overlap, there was a significant difference in the male and female SVL:HL relationships ($p = 0.01$).

Table 20. Regression results for the head length regressed against snout-vent length for each size-class. The slope of the HL:SVL regression decreased step-wise as crocodiles grew, with adults having the lowest head-length increase relative to SVL.

	Slope	SE slope	p slope	Intercept	SE intercept	p intercept	N	SE estimate	r	p estimate
Hatchlings	0.291	0.014	< 0.01	0.856	2.129	0.69	185	1.604	0.839	< 0.69
Yearlings	0.273	0.001	< 0.01	4.833	0.383	< 0.01	927	2.54	0.988	< 0.01
Juveniles	0.265	0.003	< 0.01	7.847	1.49	< 0.01	311	4.091	0.981	< 0.01
Subadults	0.239	0.004	< 0.01	26.763	3.403	< 0.01	178	6.987	0.978	< 0.01
Adult males	0.197	0.006	< 0.01	72.668	10.35	< 0.01	33	14.756	0.986	< 0.01
Adult females	0.214	0.007	< 0.01	49.808	10.444	< 0.01	42	10.426	0.978	< 0.01

C. Other populations

i. Adults

There were significant differences in the HL/SVL relationship within the Okavango adult males and females (Table 20), the St. Lucia males and females and between the two sub-populations (i.e. the samples from each location falling within the same size-range). The St. Lucia and Okavango populations exhibited different rates of increase of head length with increasing SVL for both males and females. They were:

Okavango males: SVL = 4.923 HL – 311.003 (n = 33, SE = 73.69, r = 0.986)
Okavango females: SVL = 4.483 HL – 161.492 (n = 40, SE = 47.78, r = 0.978)
St. Lucia males: SVL = 4.481 HL – 221.68 (n = 25, SE = 69.15, r = 0.972)
St. Lucia females: SVL = 3.5 HL + 151.69 (n = 31, SE = 47.35, r = 0.910)

ii. All size classes

Games (1990) provided regression results for samples (all size classes) from Lake Kariba (Zimbabwe) and the Lower Zambezi river (Mozambique) and Hutton (1987a) provided equations from Lake Ngezi (Zimbabwe). The regressions for all size classes were as follows:

Okavango: SVL = 4.07 HL – 52.84 (n = 1679, SE = 30.07, r = 0.996)
Lake Ngezi: SVL = 4.185 HL -74.038 (r = 0.99)
Lake Kariba: SVL = 3.99 HL – 54.44 (n = 219, SE = 52.75, r = 0.99)
Zambezi River: SVL = 4.1 HL – 114.70 (n = 381, SE = 84.81, r = 0.98)

The St. Lucia and Okavango populations could not be statistically compared with the Lake Ngezi sub-population as the regression statistics for this sub-population were not reported fully.

III. Head width: Snout-vent length relationships

A. Okavango crocodiles

With the exception of the adult size-class, the rate of increase of head width with SVL did not differ between sexes ($p < 0.01$) and so males and females were pooled. When the slopes for the HW:SVL regression were compared between all size classes, they were significantly different (ANCOVA, $p < 0.01$). While adult males appeared to have a higher rate of increase of HW to

SVL, but narrower heads up to an SVL of 2051 mm, the intercept was non-significant (Table 21, Figure 36).

Table 21. Regression results for head width regressed against snout-vent length for the panhandle crocodile population. With the exception of the adult size-class, the rate of increase of head width with SVL did not differ between sexes ($p < 0.01$).

	Slope	SE slope	p slope	Intercept	SE intercept	p intercept	N	SE estimate	r	p estimate
Hatchlings	0.104	0.007	< 0.01	7.153	1.064	< 0.01	185	0.801	0.742	< 0.01
Yearlings	0.124	0.001	< 0.01	3.727	0.278	< 0.01	935	1.85	0.97	< 0.01
Juveniles	0.126	0.002	< 0.01	2.537	1.088	< 0.01	311	2.995	0.956	< 0.01
Subadults	0.128	0.003	< 0.01	1.336	2.923	0.648	182	6.075	0.944	< 0.648
Adult males	0.162	0.004	< 0.01	-51.694	6.267	< 0.01	33	8.935	0.993	< 0.01
Adult females	0.143	0.006	< 0.01	-12.72	8.848	0.14	41	8.389	0.969	< 0.14

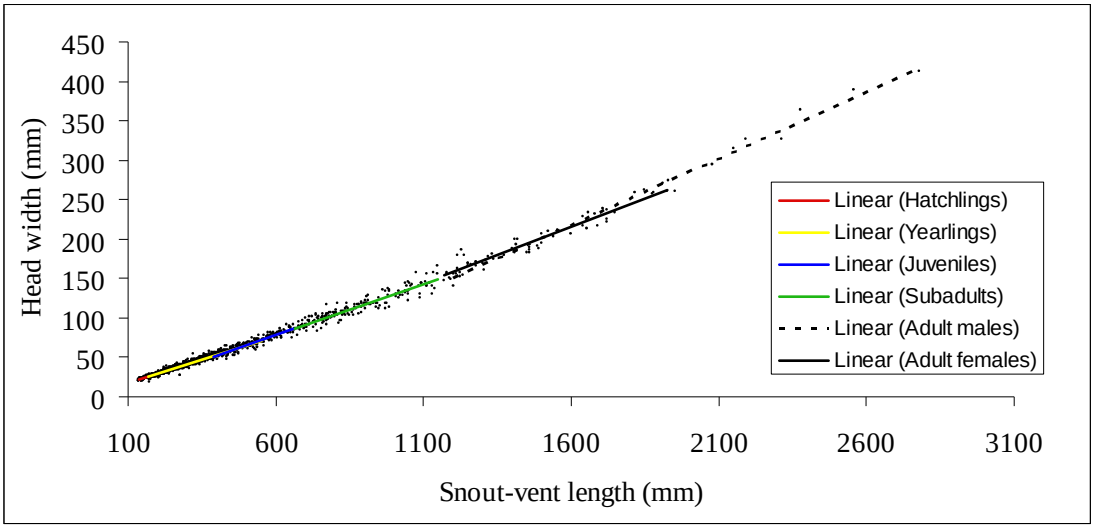


Figure 36. The relationship between HW and SVL ($n = 1638$, $r = 0.93$). Where trend lines overlap, there is a significant difference between males and females ($p = 0.01$), with males increasing in head width at a faster rate than females of the same length. Data that were obviously incorrectly recorded were excluded from the analysis.

B. Other populations

i. Adults

There was a significant difference between the Okavango adult male and female crocodiles in the SVL:HW regression, between the St. Lucia adult male and females (Leslie, 1997) and between the two sub-populations. The regression equations for the adults in the panhandle and Lake St. Lucia were as follows:

Okavango males: SVL = 5.863 HW + 327.045 (n = 33, SE = 52.7, r = 0.969)
Okavango females: SVL = 6.588 HW + 171.017 (n = 41, SE = 57.01, r = 0.969)
St. Lucia males: SVL = 6.868 HW + 560.979 (n = 25, SE = 110, r = 0.927)
St. Lucia females: SVL = 5.723 HW + 684.864 (n = 35, SE = 59.63, r = 0.856)

ii. All size classes

Games (1990) provided regression results for samples (all size classes) from Lake Kariba, Zimbabwe and Hutton (1987a) provided equations for Lake Ngezi, Zimbabwe. The regressions for all size classes were as follows:

Okavango: SVL = 7.47 HW - 2.125 (n = 1686, SE = 32.59, r = 0.99)
Lake Ngezi: SVL = 6.238 HW + 55.421 (r = 0.99)
Lake Kariba: SVL = 7.45 HW + 17.89 (n = 218, SE = 91.87, r = 0.99)

IV. Head depth: Snout-vent length relationships

A. Okavango crocodiles

The slope of the regression of HD:SVL increases more rapidly as crocodile length (SVL) increases, showing that larger animals have significantly deeper heads relative to their length than smaller animals (ANCOVA, $p < 0.01$, Figure 37, Table 22). The regression trends for juvenile and subadult size classes show significant variation in the rate of increase of HD with increasing SVL (Table 22) and so the regressions are not significant ($p = 0.14$, $p = 0.33$ respectively). The rate of increase of HD with increasing SVL did not differ between sexes ($p > 0.05$). Data that were obviously incorrectly recorded were excluded from the analysis. There was

significant variation in the HD:SVL relationship within the juvenile and subadult size classes, rendering these regressions non-significant (Table 22).

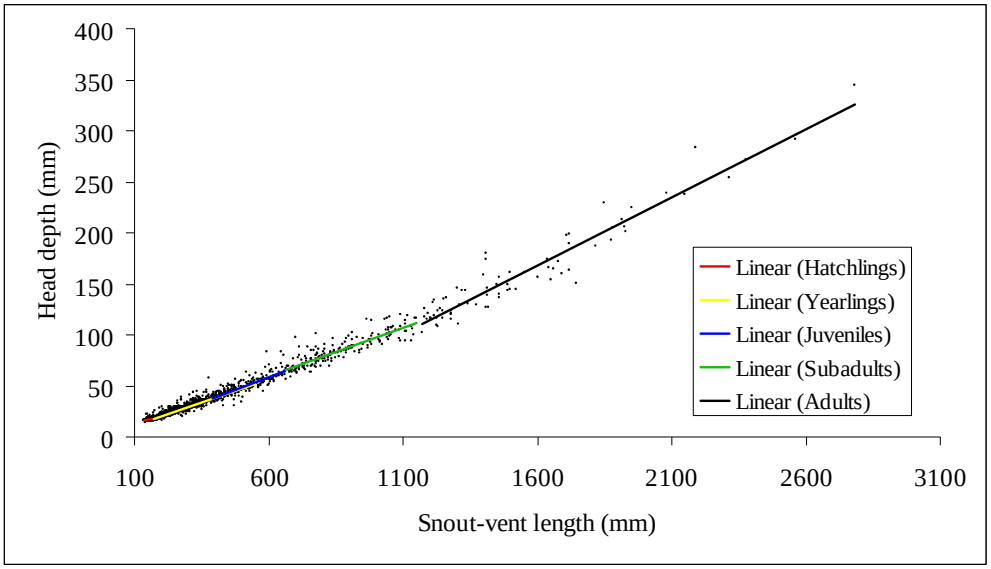


Figure 37. The relationship between HD and SVL (n = 1697, r = 0.98). The slope of the regression increases with increasing length, indicating that larger animals had significantly deeper heads relative to their length than smaller animals ($p < 0.01$). Data that were obviously incorrectly recorded were excluded from the analysis.

Table 22. Regression results for the HD:SVL regression for the panhandle crocodile population. The rate of increase of HD with increasing SVL did not differ between sexes ($p > 0.05$), although there was a significant difference between the size classes (ANCOVA, $p < 0.01$).

Size Class	Slope	SE slope	p slope	Inter-cept	SE Inter-cept	p inter-cept	N	SE estimate	r	p estimate
Hatch-lings	0.042	0.011	< 0.01	10.72	1.66	< 0.01	185	1.247	0.27	< 0.01
Year-lings	0.09	0.001	< 0.01	2.75	0.36	< 0.01	946	2.4	0.91	< 0.01
Juve-niles	0.101	0.003	< 0.01	-2.30	1.54	0.136	311	4.235	0.88	0.136
Sub-adults	0.094	0.004	< 0.01	3.27	3.35	0.33	181	6.967	0.88	0.33
Adults	0.133	0.005	< 0.01	-44.98	7.19	< 0.01	74	13.637	0.96	< 0.01

V. Snout-vent length / Total length: Snout-vent length relationships

There was no within size-class gender difference in the slope or intercept in the SVL / TL ratios regressed against SVL ($p < 0.01$) and so data were pooled for the two sexes (Figure 38). The slopes for all size classes were not significantly different (ANCOVA, $p < 0.01$). An increasing SVL / TL ratio with increasing length reflected the decreasing proportion of the total length taken up by the tail as animals grew. The highly variable nature of the hatchling size class TL:SVL ratio made the slope non-significant ($p = 0.45$, Table 23).

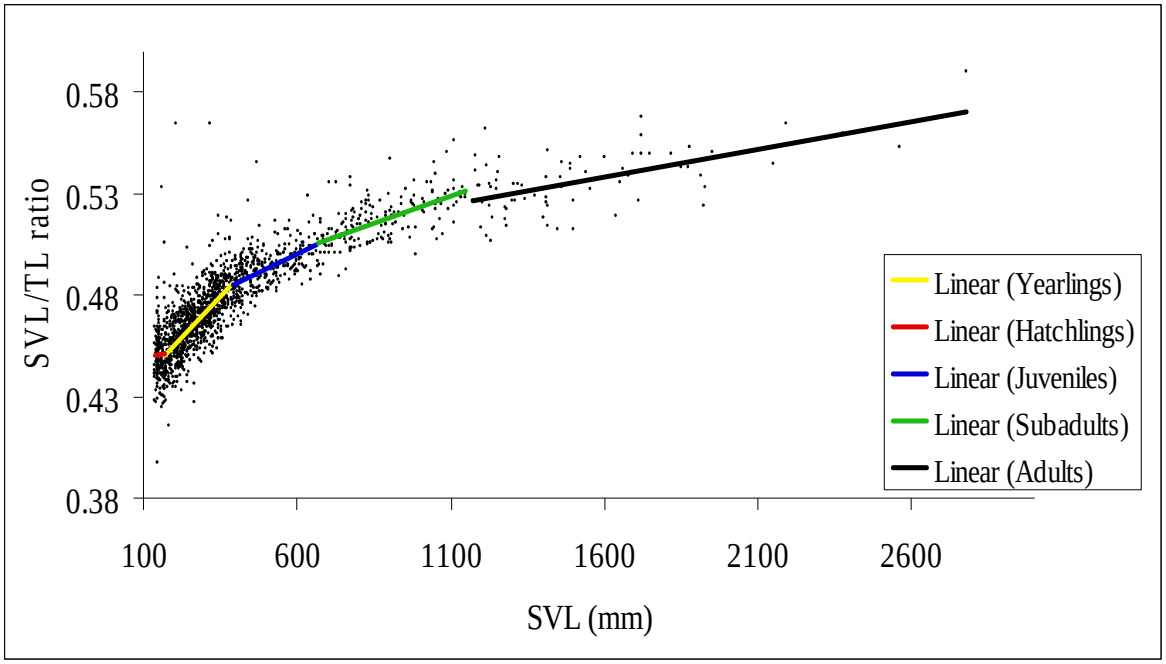


Figure 38. Relationship between the SVL / TL ratio, regressed against SVL (n = 1677). A decreasing slope signifies the reduced proportion of the TL taken up by the tail. In cases where the tail was damaged, or data were obvious outliers, these data were omitted.

Table 23. Regression results for the size class-specific SVL/TL ratio regressed against increasing snout-vent length (n = 1677). All size class-specific regressions were significant ($p < 0.05$) with the exception of the hatchlings, that were variable and showed a non-significant regression ($p = 0.45$).

	Slope	SE slope	p slope	Inter-cept	SE inter-cept	p inter-cept	N	SE estimate	r	p estimate
Hatch-lings	$3.0x10^{-5}$	$1.19x10^{-5}$	0.8	0.449	0.018	< 0.01	185	0.014	0.018	< 0.449
Year-lings	$1.64x10^{-4}$	$6.0x10^{-6}$	< 0.01	0.423	0.002	< 0.01	937	0.011	0.661	< 0.01
Juve-niles	$7.20x10^{-5}$	$7.0x10^{-6}$	< 0.01	0.457	0.003	< 0.01	306	0.009	0.527	< 0.01
Sub-adults	$5.3x10^{-5}$	$5.0x10^{-6}$	< 0.01	0.471	0.005	< 0.01	176	0.009	0.613	< 0.01
Adults	$2.7x10^{-5}$	$4.0x10^{-6}$	< 0.01	0.495	0.007	< 0.01	73	0.012	0.602	< 0.01

VI. Head length / Head width: Snout-vent length relationships

HL in hatchling and yearling crocodiles increased at a proportionally higher rate than HW, up to approximately 600 mm SVL. Juvenile crocodiles exhibited isometric growth of HL and HW, after which HW began to increase at a relatively faster rate than HL with increasing SVL (Figure 39, Table 24) in subadults and adults. However, these slopes were not significantly different from one another (ANCOVA, $P < 0.01$).

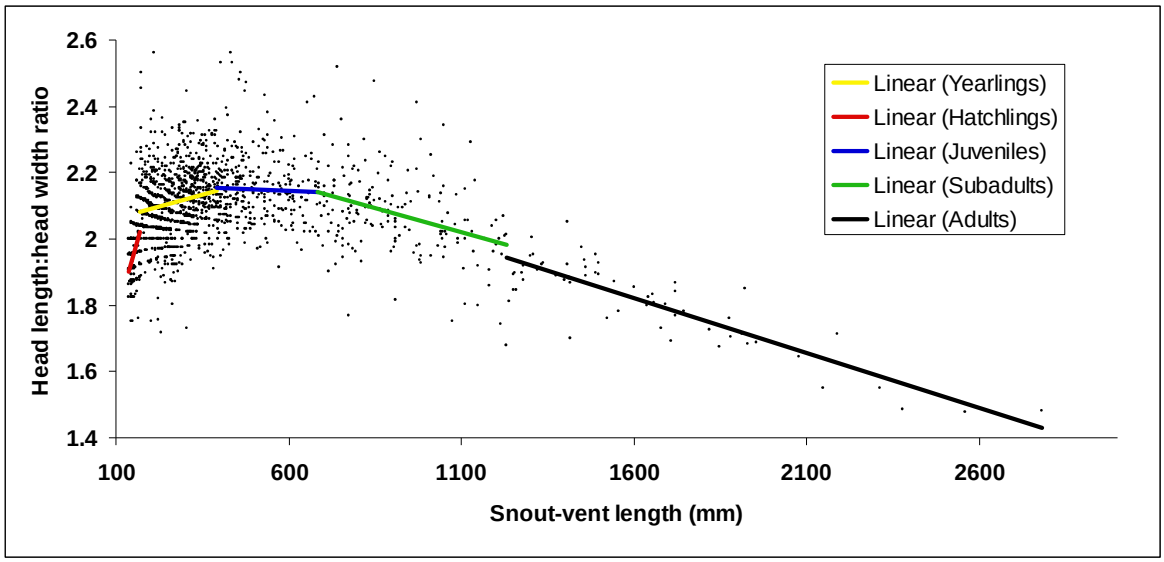


Figure 39. The HL/HW ratios for each size class, regressed against SVL for crocodiles captured in the panhandle from 2002 – 2006 (n = 1666).

Table 24. Size class specific regression results for the HL/HW ratio of crocodiles captured in the panhandle from 2002 – 2006, regressed against SVL (n = 1666).

	Slope	SE slope	p slope	Intercept	SE intercept	p intercept	N	SE estimate	r	p estimate
Hatch-lings	$3.69x10^{-3}$	$6.83x10^{-4}$	<0.01	1.400	0.104	< 0.01	185	0.079	0.370	<0.01
Year-lings	$2.92x10^{-4}$	$59x10^{-5}$	<0.01	2.032	0.016	< 0.01	920	0.110	0.160	<0.01
Juv-eniles	$-5.8x10^{-5}$	0.037	<0.44	2.178	0.037	< 0.01	309	0.102	0.044	<0.44
Sub-adults	$-2.43x10^{-4}$	$6.5x10^{-5}$	<0.01	2.304	0.057	< 0.01	178	0.117	0.270	<0.01
Adults	$-3.27x10^{-4}$	$2.5x10^{-5}$	<0.01	2.343	0.040	< 0.01	74	0.075	0.830	<0.01

VII. Head length / Snout-vent length: Snout-vent length relationships

Head length forms a large proportion of the total length in hatchlings relative to the larger size classes. The proportion of the TL made up by HL decreases as crocodiles increase in TL, with the rate of increase of HL decreasing relative to snout-vent length (Figure 40, Table 25).

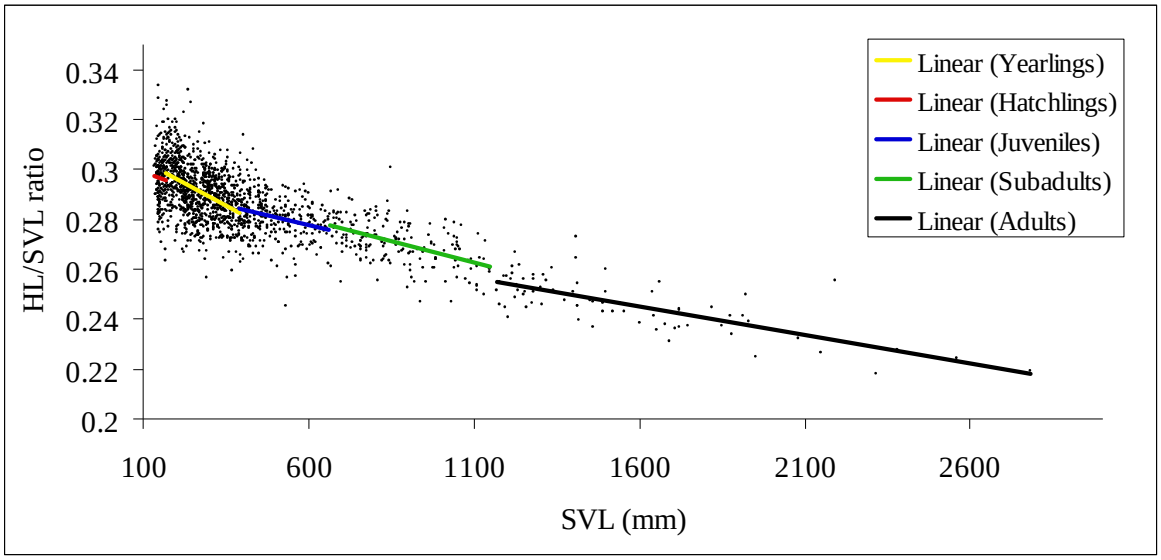


Figure 40. Size class specific relationships between the SVL / HL ratios for crocodiles captured in the panhandle region of the Okavango Delta from 2002 - 2006, regressed against SVL

Table 25. Regression results for size class specific SVL/HL ratios for crocodiles captured in the panhandle region of the Okavango Delta from 2002 - 2006, regressed against SVL.

	Slope	SE slope	P slope	Intercept	SE intercept	p intercept	N	SE estimate	r	p estimate
Hatch-lings	-4.5×10^{-5}	9×10^{-5}	0.61	0.303	0.014	< 0.01	185	0.103	0.037	< 0.037
Year-lings	-7.1×10^{-5}	5×10^{-6}	< 0.01	0.311	0.001	< 0.01	931	0.01	0.411	< 0.01
Juve-niles	-3.1×10^{-5}	6×10^{-6}	< 0.01	0.296	0.003	< 0.01	311	0.009	0.271	< 0.01
Sub-adults	-3.4×10^{-5}	4×10^{-6}	< 0.01	0.3	0.004	< 0.01	178	0.008	0.504	< 0.01
Adults	-2.3×10^{-5}	2.0×10^{-6}	< 0.01	0.281	0.004	< 0.01	75	0.007	0.731	< 0.01

VIII. Head depth / Snout-vent length: Snout-vent length relationships

The head-depth: snout-vent length ratio decreased in hatchlings (non-significant, p = 0.1) and yearlings (p = 0.01) and become isometric in the juveniles and subadults. The regression slopes for juvenile and subadult HD/SVL ratios regressed against SVL were not significantly different from zero (p = 0.21, p = 0.41 respectively). The HD/SVL ratio significantly increased with an increase in length in adults (p (slope) < 0.01, Figure 41, Table 26).

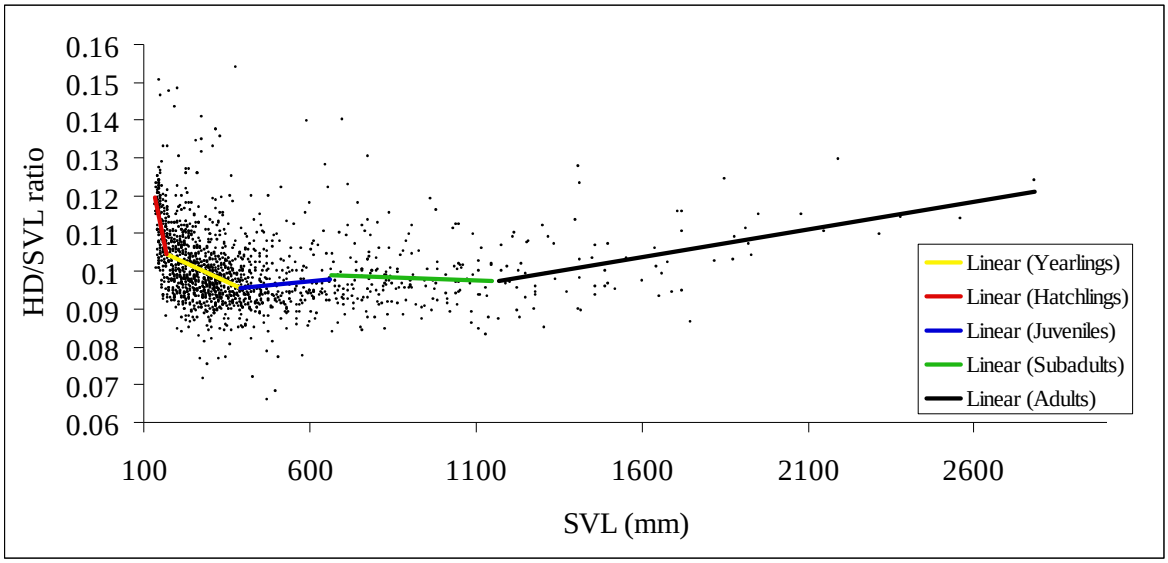


Figure 41. The relationship between the HD / SVL ratio for crocodiles captured in the panhandle from 2002 - 2006, regressed against SVL. In adults, the head become deeper relative to SVL, while in hatchlings and juveniles SVL was increasing at a relatively faster rate than HD.

Table 26. Regression results for the HD/SVL ratio for crocodiles captured in the panhandle from 2002 - 2006, regressed against SVL. It is only in the adult size class that the HD significantly increases, relative to the SVL.

	Slope	SE slope	p slope	Intercept	SE intercept	p intercept	N	SE estimate	r	p estimate
Hatchlings	$7.1x10^{-5}$	$9.0x10^{-5}$	< 0.01	0.198	0.007	< 0.01	185	0	0.018	< 0.1
Yearlings	$-4.1x10^{-5}$	$5x10^{-4}$	< 0.01	0.111	0.001	< 0.01	946	0.009	0.269	< 0.01
Juveniles	$8.0x10^{-6}$	$6.0x10^{-6}$	0.21	0.093	0.003	< 0.01	311	0.08	0.071	< 0.21
Subadults	$-4.0x10^{-6}$	$5.0x10^{-6}$	0.41	0.102	0.004	< 0.01	181	0.008	0.06	< 0.41
Adults	$1.5x10^{-5}$	$3.0x10^{-6}$	< 0.01	0.08	0.004	< 0.01	74	0.009	0.517	< 0.01

5.4.2 Growth rates

A total of 224 individuals were recaptured during the course of the project of which 116 were recaptured after a period in excess of 120 days after initial capture (Table 28). The crocodiles ranged in size (mean SVL) from 166 mm - 958 mm. Inter-capture periods ranged from 1 to 1261 days. The majority of recapture animals were yearlings (170 mm - 390 mm SVL). A number of individuals were recaptured more than once: 224 crocodiles were recaptured at least once, 44 at least twice, 7 at least three times and one was recaptured five times. Of all the yearlings that were encountered on the river during the course of the study, 81.0 % were successfully captured and a total of 75.0 % of recaptures were yearlings. The majority of crocodiles (81 %) recaptured in excess of 120 days of initial capture were yearlings ranging in size from 170 mm - 389 mm SVL (Figure 42). There were no adult recaptures.

I. Sex

Male and female growth rates were normally distributed and not significantly different (ANOVA, $F_{1,92} = 0.19$, $p = 0.66$, Figure 43). The average growth rate for yearlings with over 120 days between capture and recapture was 0.198 ± 0.116 mm.d^{-1} (approximately 72 cm.yr^{-1}).

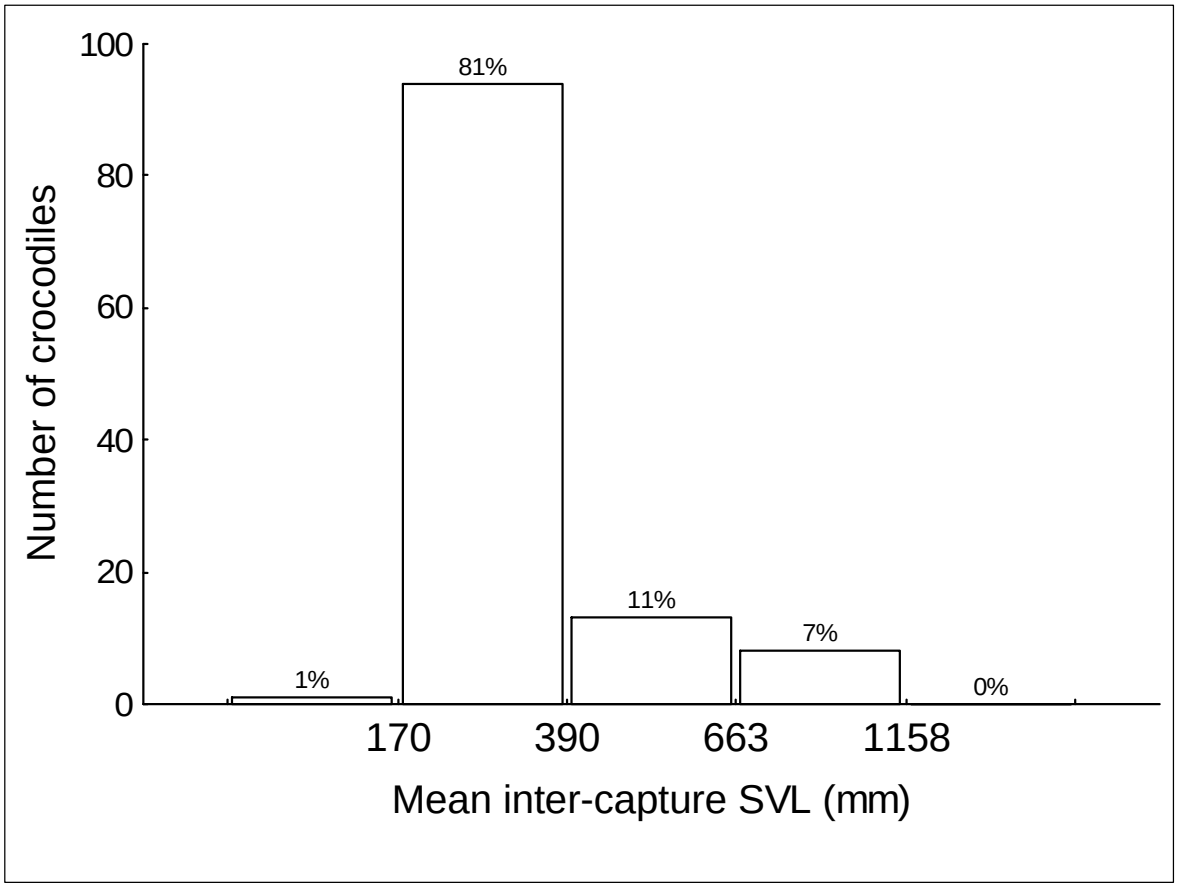


Figure 42. Frequency histogram of mean SVL of all crocodiles that were recaptured from 2002 - 2004 .

Thus, if an individuals' growth rate falls on the regression line, animals of 200 mm SVL grow at 80.23 $mm.yr^{-1}$, those of 300 mm SVL grow at 69.79 $mm.yr^{-1}$ and those of 400 mm SVL grow at 59.35 $mm.yr^{-1}$. Extrapolating the trend-line to the point where growth rate was theoretically zero yielded a maximum theoretical length of 923 mm SVL, which was the maximum length of these animals under this continued rate of growth (Figure 44).

Overall, growth rate (GR) was negatively correlated with increasing SVL (Figure 44). There was a large variation in growth rate between smaller crocodiles ($r = 0.15$) and the regression was not significant ($p = 0.15$). The equation describing the regression of GR against SVL was:

$GR = -2.86x10^{-4}$ SVL + 0.277 $mm.d^{-1}$ ($n = 94$, $SE = 0.115$, $r = 0.146$, $p < 0.15$, Figure 44).

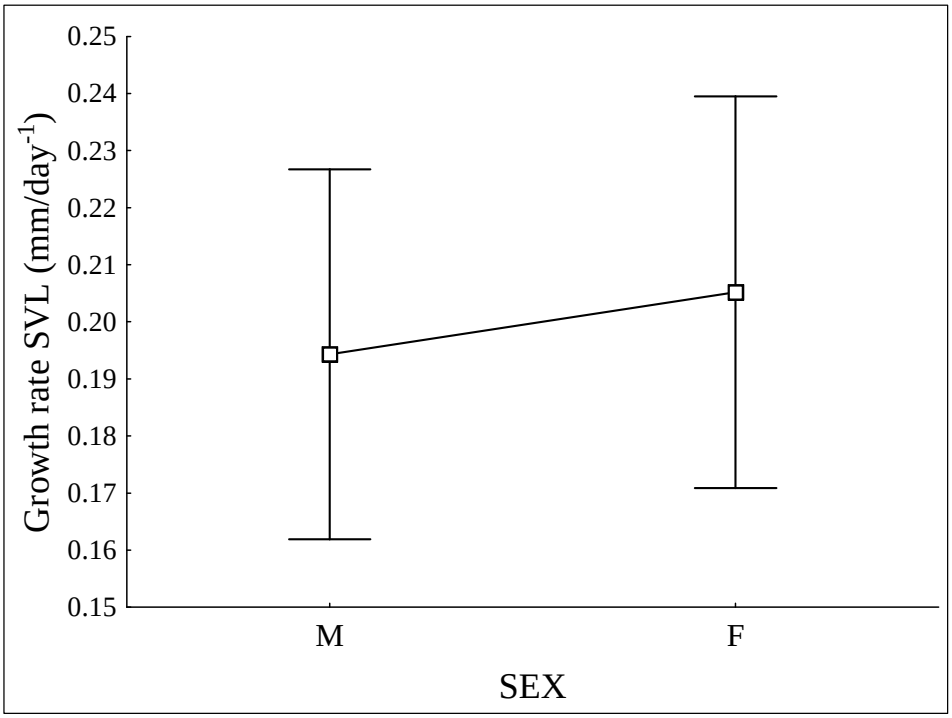


Figure 43. Comparison between male and female growth rates for all animals recaptured in the panhandle region of the Okavango Delta from 2002 - 2006. There was no significant difference between male and female growth rate (p = 0.66).

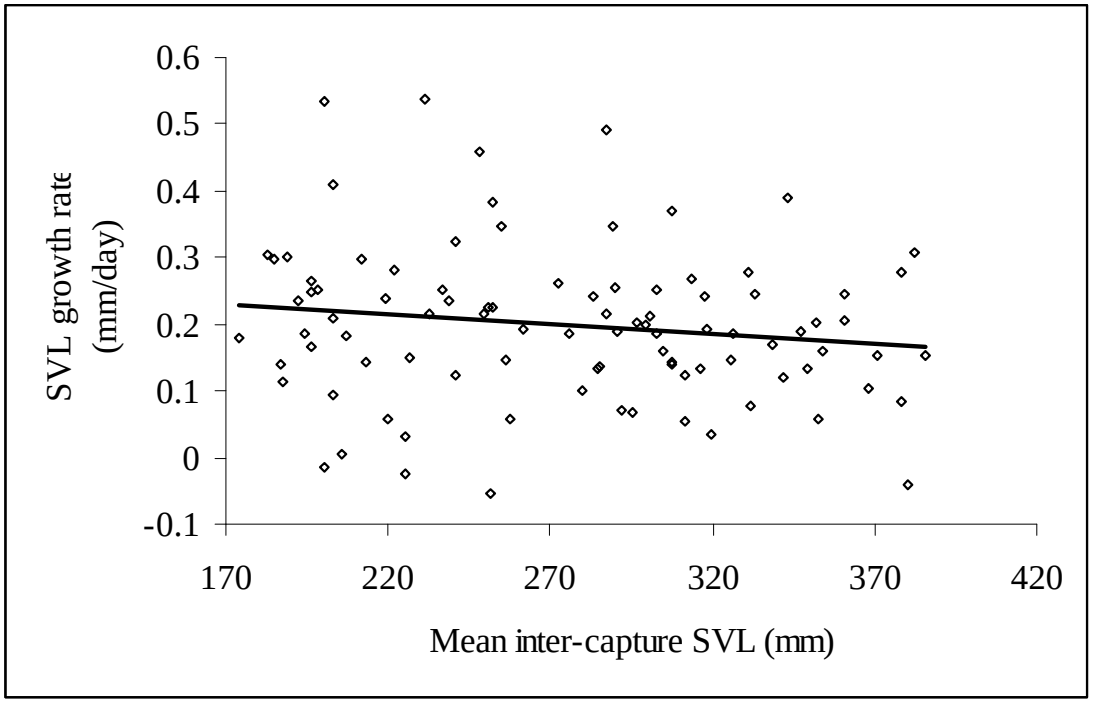


Figure 44. Regression of SVL against mean SVL during the inter-capture period for all crocodiles recaptured in the panhandle region of the Okavango Delta during the study.

II. Water temperature

The average water temperature over the three year period was 22.5 ^{0}C and the sinusoidal, time-series equation to describe the best-fit line through these data was:

$$Yt = 22.85(5.53233\cos \omega t + 0.92939\sin \omega t)$$

where:

$$\omega = 2\pi f$$

The fitted curve, with an R^2 value of 86.2 %, intersected the average temperature line at 104 and 280 days (2003), 469 and 645 days (2004) and 834 and 1010 days (2005) after January 1, 2003 (Figure 45).

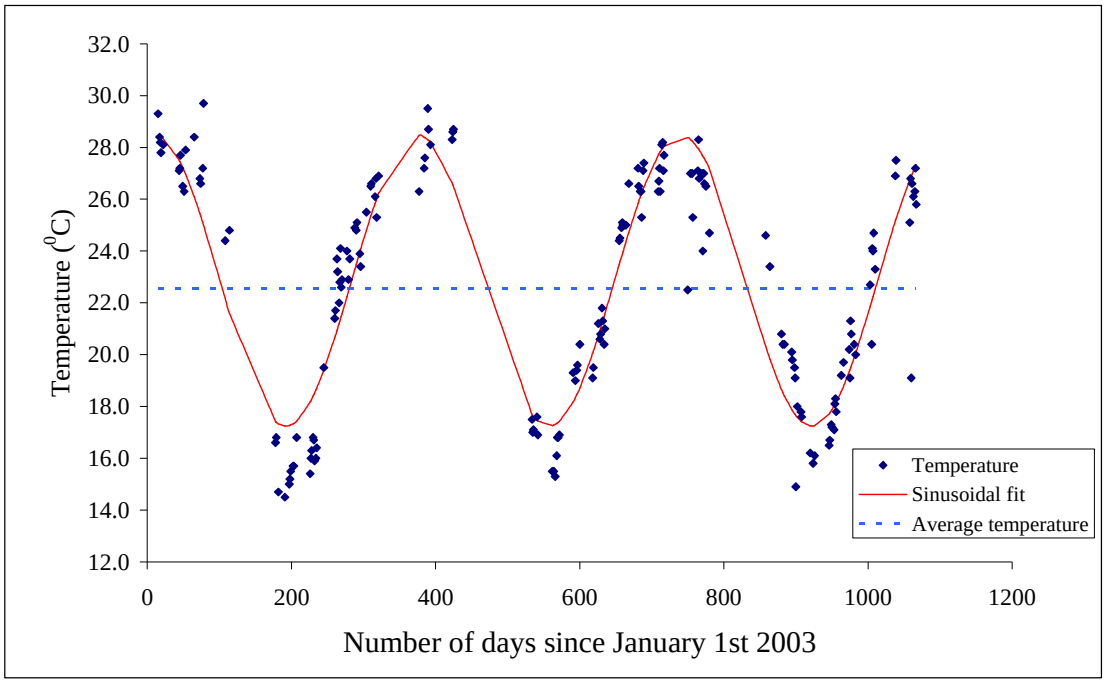


Figure 45. Sinusoidal, time-series equation to describe the best-fit line through water temperature data, recorded between the hours of 22h00 and 02h00 during night shifts, using a BATT-12 thermocouple meter (Physi-temp, CA, USA).

Growth rate was not significantly correlated to either inter-capture time in above-average air temperature ($\beta = 0.11$, $p = 0.23$) or water level ($\beta = 0.11$, $p = 0.26$), although these parameters were significantly correlated to water temperature (air temperature, water level: $\beta = 0.42$, -

0.49, p > 0.05). The effect of seasonality was therefore represented by "growth periods", when the water temperature was above average.

The period of time the crocodiles were exposed to above-average water temperatures (growth period) between captures significantly and positively influenced growth rate (Correlation: β = 0.37, P > 0.001). A linear regression confirmed this relationship (Figure 46). The regression equation for this relationship was:

GR = 0.267 PwT + 0.075 (n = 94, SE = 0.107, r = 0.386, p < 0.001).

Over the three year period of the project during which water temperature was accurately measured, it was above average (22.5 ^{0}C) 51.8 % of the time. Thus, in any given year, the growth rate of an average yearling falling on the regression line would be an average of 0.213 mm.d^{-1}, or 77.86 mm.y^{-1}.

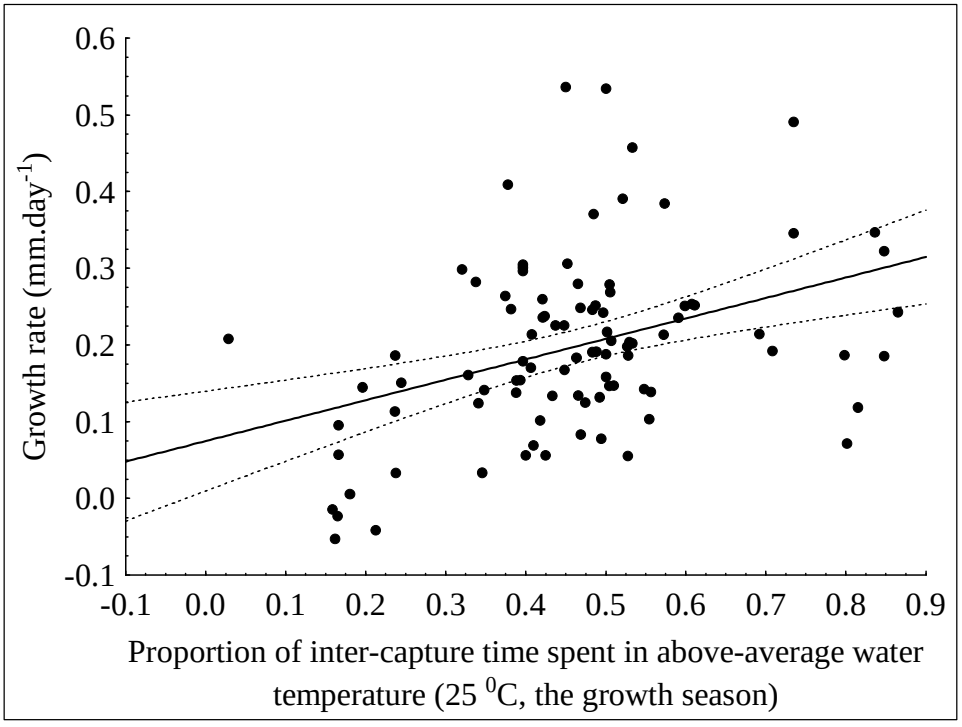


Figure 46. The effect of inter-capture time spent in above-average water temperatures ("Growth season" [GS]; > 22.5 ^{0}C) on growth rate (GR) for all recaptured crocodiles in the panhandle region of the Okavango Delta from 2002 - 2006.

When the influence of seasonality was controlled for, by plotting the residual values from Figure 46 against mean inter-capture SVL, the isolated influence of the length of the

individual was apparent. This illustrated the fact that the size of the animal influenced its GR in that GR significantly decreased as crocodiles increased in length irrespective of seasonal effects (Figure 47). The regression equation was:

GR = -5.0×10^{-4} SVL + 0.142 mm.d^{-1} (n = 94, SE = 0.103, r = 0.286, $p < 0.01$) (Figure 47).

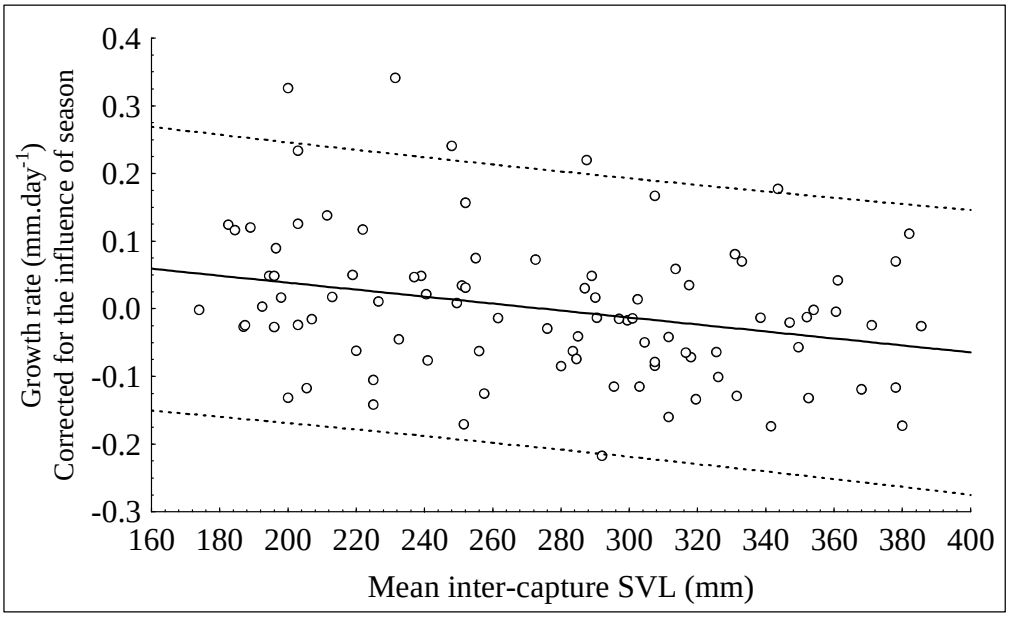


Figure 47. The relationship between the CGR and SVL for all the crocodiles recaptured in the panhandle from 2002 - 2006.

5.4.3 Body condition indices

I. Okavango population

Condition indices (Games, 1990) using neck and base of tail circumferences, were not normally distributed and non-parametric Mann-Whitney U tests were performed to test for differences between season and sex within the Okavango population. Relative condition factors (RCF) were normally distributed and t-tests were used to test for differences in sex and season. Table 27 summarizes results for the regressions between body mass against SVL, RCF and condition indices (CI) for both neck and base of tail circumferences.

Hatchlings were, with the exception of two animals, caught in the “growth” season (8 October-15 May) and as it was difficult to sex these animals reliably in the field, no comparisons between sex and seasons could be made. Both yearling males and females

showed significantly different condition indices with regards to season when using both neck circumference (females, $p = 0.002$, males, $p = 0.006$) and base of tail circumference (females, $p = 0.02$, males, $p = 0.007$). Significantly higher CI's were apparent in the growing season (Table 27). Juvenile females had a lower CI's in the growing season (BTC CI = 4.04, $p = 0.006$, neck CI, $p = 0.001$) compared to the non-growing season (BTC CI = 4.18). Juvenile males had higher tail-base CI's in the non-growing season (BTC CI non-growing season = 4.12; BTC CI growing season = 4.06; $p = 0.04$), with no difference in the neck CI's. Subadult and adult animals did not show any differences in condition indices with regards to season ($p > 0.05$).

With the exception of subadults, where females had significantly higher tail-base CI's than males ($p = 0.03$) during the growth season, sex did not have any significant effect on condition indices ($p > 0.05$).

The relative condition factor (RCF) correlated significantly to all other indices of condition (Table 28) and was most highly correlated to the residual index (0.99, $p << 0.01$). The two indices were highly correlated and for this reason, only RCF will be further discussed. There were no seasonal or sex-related differences with regards to RCF calculated for individuals (Figure 48). The different size classes were not significantly different from one-another (ANOVA, $p = 0.08$). RCF values were then calculated for crocodiles recaptured from 90 – 365 (i.e. within a year, or at least one full season) and correlated significantly to the proportion of inter-capture time spent in above-average water temperature (Correlation = -0.27), water level (Correlation = 0.31) and air temperature (Correlation = -0.33) (Table 28).

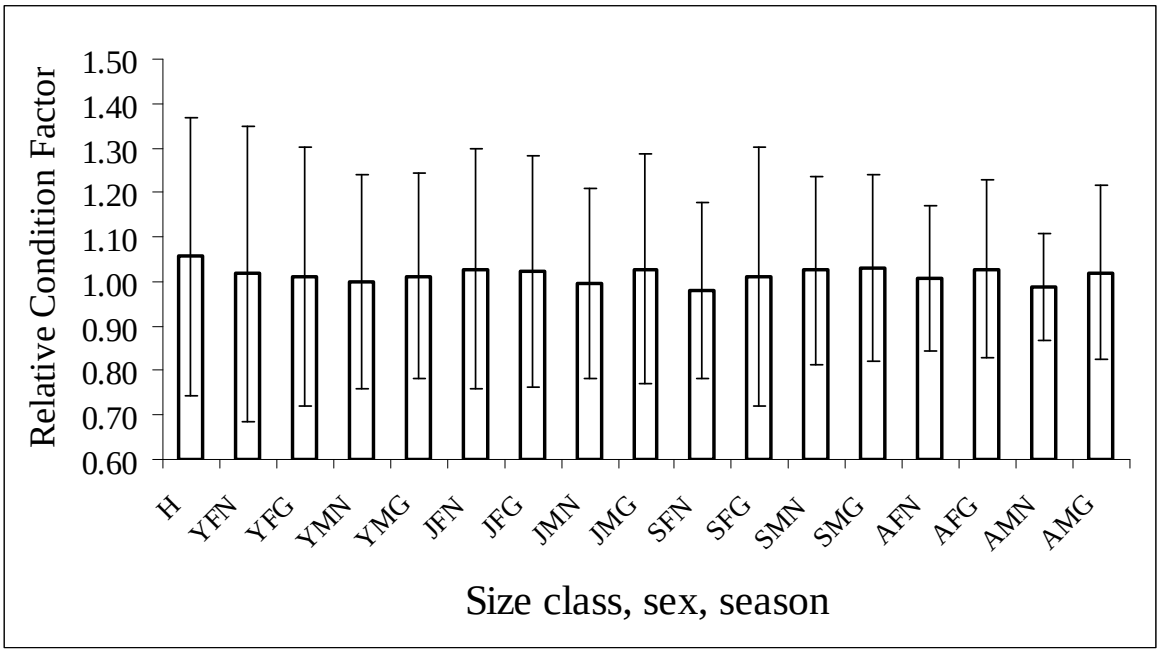


Figure 48. RCF values for each size-class (Hatchling, Yearling, Juvenile, Subadult, Adult), sex (Male, Female) and season (Growth, Non-growth).

Table 27. Results from the Ln (mass) vs Ln (SVL) regression and condition indices for each size-class, sex and season for all crocodiles recaptured in the panhandle region of the Okavango Delta from 2002-2006.

Size class Sex Season	Inter-cept	SE Inter-cept	p inter-cept	Slope	SE Slope	P slope	RCF	SD RCF	CI BTC	SD CI-BTC	CI NC	SD CI-BTC	N
H	-19.07	0.63	< 0.01	3.38	0.07	< 0.01	1.06	0.31	3.89	0.27	4.03	0.30	182
YFN	-17.37	0.75	< 0.01	3.20	0.08	< 0.01	1.02	0.33	3.82	0.33	3.83	0.30	149
YFG	-16.74	0.54	< 0.01	3.11	0.07	< 0.01	1.01	0.29	4.38	0.29	4.42	0.28	183
YMN	-18.46	0.45	< 0.01	3.32	0.06	< 0.01	1.00	0.24	3.74	0.24	3.74	0.23	293
YMG	-16.58	0.38	< 0.01	3.09	0.05	< 0.01	1.01	0.23	3.77	0.23	3.78	0.26	236
JFN	-14.30	1.10	< 0.01	2.85	0.12	< 0.01	1.03	0.27	4.18	0.27	4.13	0.27	36
JFG	-18.77	0.57	< 0.01	3.37	0.07	< 0.01	1.02	0.26	4.04	0.26	3.93	0.28	85
JMN	-18.42	0.83	< 0.01	3.31	0.09	< 0.01	1.00	0.21	4.12	0.21	4.04	0.24	65
JMG	-16.74	0.54	< 0.01	3.11	0.07	< 0.01	1.03	0.26	4.06	0.26	3.99	0.26	126
SFN	-17.04	1.41	< 0.01	3.16	0.15	< 0.01	0.98	0.20	4.38	0.20	4.46	0.25	41
SFG	-18.18	1.31	< 0.01	3.29	0.13	< 0.01	1.01	0.29	4.38	0.29	4.42	0.28	58
SMN	-16.59	2.07	< 0.01	3.12	0.21	< 0.01	1.03	0.21	4.34	0.21	4.46	0.29	32
SMG	-16.94	1.18	< 0.01	3.16	0.12	< 0.01	1.03	0.21	4.28	0.21	4.36	0.23	50
AFN	-14.17	6.92	NS	2.90	0.67	NS	1.01	0.16	4.66	0.16	4.71	0.31	6
AFG	-4.83	8.04	< 0.01	1.99	0.78	NS	1.03	0.20	4.64	0.20	4.72	0.30	11
AMN	-59.99	15.60	NS	7.36	1.52	NS	0.99	0.12	4.74	0.12	4.90	0.22	4
AMG	-21.91	4.49	< 0.01	3.63	0.43	< 0.01	1.02	0.19	4.60	0.19	4.71	0.22	10

Table 28. Correlations between abiotic factors and condition indices for animals recaptured from 90 - 365 days after initial capture. PwT, PwL and PwA refer to the proportion of inter-capture time the individuals spent in above-average water temperature, water level and air temperature. Significant values ($p < 0.05$) are emphasised in bold text.

	PwT	PwL	PwA	Res-iduals	RCF	CI (tail)	CI (neck)
PwT	1.00						
PwL	**-0.50**	1.00					
PwA	**0.52**	**-0.55**	1.00				
residuals	**-0.25**	**0.31**	**-0.33**	1.00			
RCF	**-0.27**	**0.31**	**-0.36**	**0.99**	1.00		
CI (tail)	0.01	-0.07	-0.05	**0.45**	**0.47**	1.00	
CI (neck)	-0.07	0.02	-0.12	**0.48**	**0.51**	**0.86**	1.00

The increase in condition reflected by the RCF values was significantly and positively correlated to a rise in water-level and negatively correlated to time spent in above-average water and air temperatures (Figure 49). Average RCF values were intersected when animals had spent 50 % of their time in above-average temperatures and water level.

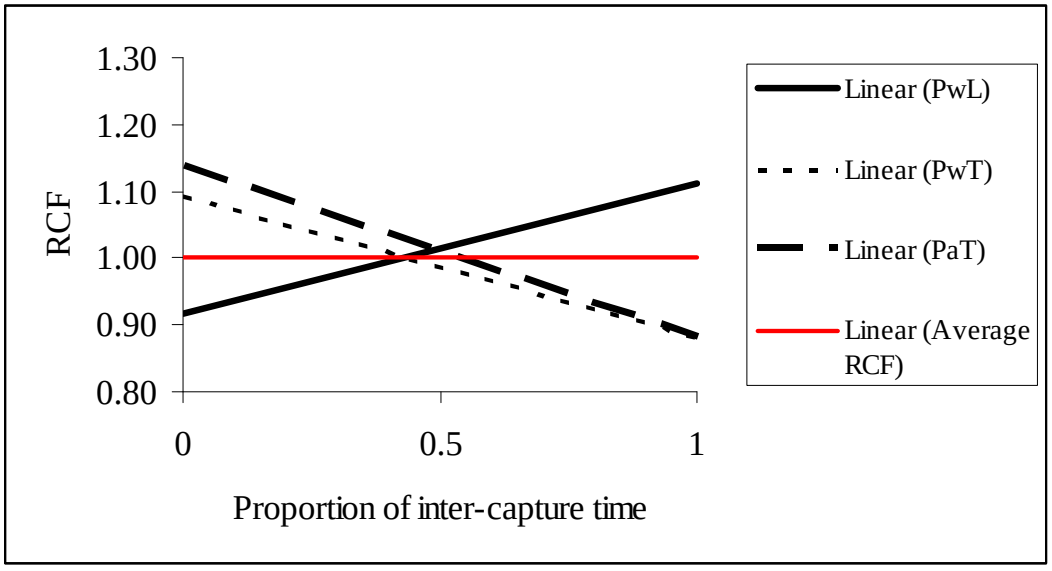


Figure 49. Regression lines for relative condition factor (RCF) against the proportion of inter-capture time the crocodiles were exposed to above-average water level (PwL), water temperature (PwT) and air temperature (PaT).

5.5 DISCUSSION

5.5.1 Morphometrics

As crocodiles increase in length, the rate at which snout-vent length increases relative to total length may be an indication of their habits. Small crocodiles have relatively longer tails than large crocodiles. They need to be highly mobile to capture fast-moving invertebrate prey, in addition to being able to manoeuvre quickly and efficiently to avoid capture by predators. As they increase in size, the numbers of potential predators decreases to eventually just humans and other crocodiles. Large crocodiles feed less often, on fewer, larger prey items and do not need to feed as regularly as smaller crocodiles that feed constantly throughout the year in the panhandle (Wallace & Leslie, 2007, in Press).

Larger animals grow in girth at a much faster rate relative to an increase in length than do smaller animals. This added girth and mass is an adaptation that is required to subdue large mammalian prey. In areas where crocodile populations have historically been exposed to a flowing water system, such as the Okavango and Zambezi River systems, the adult crocodiles also have significantly longer tails than in those areas, such as the Lake St. Lucia system, where a constant flowing current is not an issue[19]. While the differences in tail length between the adult crocodile populations of the Okavango and St. Lucia systems may seem negligible (106 - 131 mm shorter), it may be possible that this length difference was an indication of more basic differences in tail shape (Webb & Messel, 1978b). A small increase in tail length may possibly provide an animal with a distinctive swimming advantage. The sexual dimorphism shown in adult Okavango crocodiles may be indicative that the larger males, with their relatively longer tails, are more mobile than the females. This has been shown in *C. porosus* (Webb *et al.*, 1977; Webb & Messel, 1978b) and *A. mississippiensis* (Joanen & McNease, 1970, 1972). In Zimbabwe, mature females were restricted to breeding areas, while males ranged more widely and had non-overlapping ranges (Hutton & Woolhouse, 1989). These reports were not conclusive regarding whether these ranges were defended or not by the adult males. Similarly, adult *C. porosus* females occupied core areas centred around nesting sites, and adult males moved in search of females occupying these core areas during the mating season (Kay, 2004b).

[19] Lake St. Lucia, an estuarine system, is affected by tides, and while there may be current associated with the tides, the greater lake does not experience a permanent current.

No sexual size dimorphism was shown in juvenile and subadult animals in the Okavango population (Detoeuf-Boulade, 2006). Adult males, however, grew larger than adult females and adult females had relatively longer heads than adult males of the same total length.

Crocodilians such as *Mecistops cataphractus* and *Gavialis gangeticus*, with long, thin jaws are morphologically adapted for a predominantly fish diet, although these species are fairly opportunistic and will also feed on amphibians and invertebrates (Richardson *et al.*, 2002). However, they are not suited to taking large mammalian prey. The ontogenetic shift in body proportions in the panhandle crocodiles extends to skull morphology, where small animals have snouts that increase in length at a proportionally faster rate than the body does. It has been suggested that this is an adaptation to capturing smaller, faster prey items (Wallace, 2006; Wallace & Leslie, in Press). The shift in diet from invertebrates to predominantly fish at approximately 400 mm SVL (Wallace, 2006; Wallace & Leslie, in Press) coincides with a broadening of the muzzle, an adaptation to managing larger, stronger prey items such as larger fish species. Hutton (1987a) noted that crocodiles from Lake Ngezi undergo a similar shift in diet at 600 mm SVL and Games (1990) reported the shift in the Lake Kariba population at 700 mm SVL. Webb and Messel (1978a) reported this allometric increase in head width in *C. porosus*, a close relative of *C. niloticus*, at around 800 mm SVL and cite similar changes from for *C. acutus* and *Caiman sclerops* (Mook, 1921) (cited in Webb & Messel, 1978a).

The proportional rate of growth of HD to SVL decreased in hatchling and yearling animals was isometric in juveniles and subadult animals and then increased again in adult animals. The predominance of fish in the diet of juvenile and subadult animals (Hutton, 1987a; Wallace & Leslie, in Press) may mean that these animals do not need the extra strengthening of the jaw brought about by the allometric increase of the depth of the jaw. The associated increase in surface area for muscle-attachment with increased head depth would give larger animals a distinct advantage to handle larger mammalian prey, as well as providing the extra strength to withstand powerful knocks to the skull by these prey. The swift ontogenetic shift in skull morphology does therefore not seem to be restricted to smaller animals (HW and HL), but also occurs at the onset of sexual maturity (HD) to prepare adults for larger prey.

5.5.2 Growth rates.

In this study, recaptures were restricted to animals less than 1000 mm SVL. Sex-related differences in growth rates were still not apparent at this size and this finding is similar for other populations of *C. niloticus* (Hutton, 1987a; Games, 1990), *C. porosus* (Webb *et al.*, 1978; Kay, 2004b) and *A. mississippiensis* (Brandt, 1989). Games (1990) found this to be the

case for animals less than 500 mm SVL from Lake Kariba and the Lower Zambezi River, as determined by skeletochronology. In ectotherms, abiotic factors play an important role in growth rates and under optimal pen densities, feeding and temperature conditions, captive crocodiles will grow faster than those in the wild (Hutton *et al.*, 1987), sometimes doubling growth rates of animals in the wild (Chabreck & Joanen, 1979). The effects of measured abiotic factors contributing to the growth rates were therefore assessed to account for some of this variation.

Overall, growth of these size classes was highly variable. This individual variability in growth rates is a common feature for juvenile *C. porosus* (Webb & Messel, 1978a; Kay, 2004b) and other crocodilians (Hutton *et al.*, 1987). Hutton (1987b) reported average growth rates of 100 mm per year for the first four years of life (cited in Games, 1990).

Webb *et al.*, (1978) showed that the proportion of inter-capture time spent in a longer "dry" season, associated with warmer temperatures, increased the growth rate of *C. porosus.* Water temperature is probably far more important than air temperature in determining crocodilian activity and growth (Webb & Messel, 1978a; Hutton, 1987a). Games (1990) used a lake water temperature of 24 ^{0}C as his "non-growing" period, a period of four months from the beginning of May to the end of August. During flooding, water inundated the surrounding floodplains, providing a rich supply of food, most especially invertebrates and many of the resident fish species that made use of this flooded habitat to breed. The flooding of the Okavango River system allowed crocodiles to exploit new feeding areas for extended periods of time during the wet season and this, associated with warmer water temperatures, increased growth-rates. This was similar to the findings of Webb *et al.*, (1978) in the Liverpool river system (although the flooding was probably not as extreme), where water levels rose with the onset of the wet season and growth-rates increased.

A crocodile specimen from Ngamiland (presumably from the Okavango Delta) was aged by examining the dorso-lingual region of the dentary and was found to be in its fifth year of growth (Pooley, 1962). Seasonal variation in the formation of the bone was obvious and the specimen had a TL of 810 mm (approximately 390 mm SVL). Assuming this was an average-length hatchling (153 mm SVL), it had grown approximately 237 mm in its first four years, at an average of approximately 59 mm.y^{-1}. This animal was at the upper size-limit of the yearling size class and its growth rate was very similar to that calculated for animals of this size in this study (59.35 mm.yr^{-1}). Games (1990) found that an SVL of 500 mm was attainable in four years in Lake Kariba, suggesting a lower growth rate than the Okavango River. This

was attributed to a slow growth rate of juveniles in the first two years, perhaps due to the absence of crustaceans in Lake Kariba. After the first two years, the increased quantity of prey items in the stomach suggested that the crocodiles had become more efficient predators and growth rates increased correspondingly. Webb *et al.,* (1978) found a similar trend of decreasing growth rate with increasing size in *C. porosus* below 800 mm SVL. Growth rates increased with the shift in feeding preferences at this size. The Okavango system has no paucity of available prey for the smaller animals, although *C. niloticus* in the Okavango panhandle show this dietary shift at approximately 400 mm SVL, which is two-thirds the length of crocodiles from Lakes Ngezi (600 mm SVL) and Kariba (700 mm SVL). This early shift in diet may have allowed the panhandle crocodiles to maintain their growth rates throughout early years of life, with the abundance of larger fish making it more energetically viable to alter feeding habits at a smaller size than in other African studies. The theoretical maximum length of *C. porosus* in the above study (Webb *et al.*, 1978) calculated by extrapolating growth rates was 1140 mm SVL for males and 990 cm SVL for females. The Okavango yearlings had a theoretical maximum length of 923 mm SVL. These were clearly under-estimates and the possible reason for this, suggested by Webb *et al.,* (1978), was the distinctive shift in diet to more energetically productive prey as the crocodiles increased in size. The theoretical maximum length of 923 mm SVL may have been the maximum point at which it was no longer energetically feasible to feed on such small prey items.

The lack of adult recaptures reflects the ability of larger animals to avoid recapture (become trap-shy). Crocodilian growth rates are highly variable and therefore size-age curves show large errors if they are used to predict the age of individuals (Hutton, 1987c). However, given the variability in growth rates of juvenile animals, it is not possible to accurately estimate age using regression methods. Brandt (1989) found this in *A. mississippiensis,* Games (1990) in C. *niloticus* and Webb *et al.* (1978) and in *C. porosus* (Kay, 2004a).

5.5.3 Body condition indices

Traditionally, SVL was used as the basic index of body size (Webb & Messel, 1978a) because TL relied on the assumption that the tail was undamaged. However, this was not always the case. In addition, Webb and Messel (1978a) found that tail length was slightly sexually dimorphic. Body mass varies with the amount of food in the stomach (Webb *et al.*, 1978) and is therefore not a reliable indicator of growth. While SVL growth of panhandle crocodiles was, for the most part, significantly correlated to the proportion of time spent in above-average water temperatures, the increase in condition for hatchling, yearling and juvenile animals was positively correlated to a rise in water level and negatively correlated to time

spent in above-average water and air temperatures. Interestingly an increased proportion of time spent in warmer than average water and air temperature decreased the RCF, while the proportion of time spent in above-average water level increased the RCF. This was probably due to the fact that in above average temperatures, energy was being put into active growth of the crocodiles, whereas in the high - water season, the over-abundance of food allowed the crocodiles to improve physical condition.

Games (1990), found that juvenile crocodiles did not differ significantly in RCF values between sex, age, differing parasitic loads or the timing of the hot, wet season. However, RCF values differed between cool and warm periods. These findings showed that RCF values for juveniles were higher in the cool, dry period, due to higher water levels allowing crocodiles to exploit new food sources. Similar opportunistic use of "blooms" of prey by crocodilians has been documented (Gorzula, 1978; Taylor, 1979; Webb *et al.*, 1982; Webb *et al.*, 1991). The quantity and type of prey ingested has direct consequences for body condition. *Crocodylus porosus* juveniles showed similar growth rates, in different studies, when they had similar diets (Webb *et al.*, 1991). In American alligators, even when temperatures were maintained at 28 ^{0}C, blood glucose levels in summer exceeded those in winter, when appetite was decreased. Metabolic rates were closely correlated to blood glucose levels and animals stopped feeding and growing in winter (Coulson & Hernandez, 1964). The same study noted a decline of condition factor during the summer months in juvenile alligators and attributed this to a combination of growth and higher metabolic costs as a result of higher temperatures. In the beginning of autumn, as temperature and metabolic costs began to decrease, but food availability and consumption did not, body condition improved (Coulson & Hernandez, 1964)

The panhandle juveniles RCF values averaged 1.01 in the non-growing season and 1.02 in the growing season, slightly lower than juveniles from the Ume estuary (Lake Kariba, Zimbabwe), which averaged 1.1 (Games, 1990). The panhandle adults had an average RCF of 1.02 in the growing season and 1.0 in the non-growing season. These values compare with the St. Lucia adults, whose RCF values averaged 1.0 (n = 40). Ume estuary adults and subadults had average RCF values of 1.15 in the warmer season and 1.17 in the cooler season.

It is therefore possible that external factors, such as the continually flowing nature of the Okavango River, may act to increase day to day energy expenditure and reduce the amount of stored fat in the panhandle crocodiles.

5.6 Conclusion

A number of biotic and abiotic factors interact to determine growth rates, morphometrics and body condition indices of crocodilians. In the Okavango panhandle, the most significant influences were water level and temperature, diet and possibly the fast-flowing nature of the river itself. While these influences were not unique to this crocodilian population, their combined effects may distinguish the physical characteristics of the individuals making up the panhandle population from other populations. The body design of crocodilians, while showing extreme conservation throughout their evolution, are phenotypically flexible which may allow for minor adjustments in response to environmental stimuli, as demonstrated by extant genera (Richardson *et al.*, 2002).

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CHAPTER 6.

AN INVESTIGATION INTO THE MOVEMENT OF CROCODILES IN THE OKAVANGO PANHANDLE, USING CAPTURE-MARK-RECAPTURE TECHNIQUES AND A PILOT STUDY USING RADIO-TELEMETRY TECHNIQUES

6.1 ABSTRACT

A mark-recapture study within the panhandle region of the Okavango Delta, Botswana resulted in a total of 1717 individual crocodiles captured from January 2002 to December 2006, of which 272 were subsequently recaptured at least once. Four of these animals were hatchlings (< 170 mm SVL), 215 yearlings (170 - 389 mm SVL) and 49 juveniles (390 - 663 mm SVL). Of all captures, 56 % of the animals captured and 75 % of recaptures were yearlings with a median inter-capture period of 85 days. The time between recaptures ranged between one and 1074 days and distances travelled ranged between 0 and 77 903 m. Generally the crocodiles showed no significant differences between sexes in terms their size, the distances they travelled, either in total or by day. Overall, 87.9 % of recaptures moved less than 5000 m from the point of initial capture, 71.7 % moved less than 1000 m and 62.5 % of crocodiles moved less than 500 m. Telemetry results for two adult males and two adult females showed that adults in the panhandle occupy definite ranges, within which were preferred core areas where the majority of their time was spent. One male remained within 300 m from the location at which he was tagged. The other male patrolled a territory along 5 km of the main channel within the precisely overlapping 11.2 km area occupied by the two females. Both females spent the breeding season at nesting sites.

6.2 INTRODUCTION

Animal movement patterns need to be assessed to understand basic population processes and can themselves be important demographic processes (Hutton, 1989). Most crocodilians show low spatial movement patterns throughout their lives (Webb & Messel, 1978; Magnusson, 1979b; Webb *et al.*, 1983; Hutton, 1989; Tucker *et al.*, 1997a; Tucker *et al.*, 1997b; Tucker *et al.*, 1998; Munoz & Thorbjarnarson, 2000) and these are mainly closely associated with their life-history stage and gender (Kay, 2004a). Dispersal is the movement of individuals away from the area in which they spent the initial part of their lives (Hutton, 1989). Innate dispersal is spontaneous, genetically determined and generally random whereas environmental dispersal is often short and directional resulting from the avoidance of unfavourable habitat or social conditions (Hutton, 1989). Separation of juveniles from adults appears to be ecological in the natural environment (Cott, 1961; Pooley, 1982; Hutton, 1989) and may result from the threat of cannibalism. To reduce conflict or cannibalism there may be movement or segregation of individuals based on their size (Hutton, 1984; Kofron, 1993b; Letnic & Connors, 2006). Dispersal of Nile crocodiles away from the nesting areas in Lake Ngezi, Zimbabwe, occurred at around 120 cm total length (Hutton, 1989). Juvenile animals moved mostly in summer, ranging significantly further than in winter. Crocodiles over 120 cm may have been excluded by adults, while smaller animals were still accepted. Larger crocodiles ranged increasingly widely and the largest non-breeders had no distinct centre of activity. Mature, breeding females typically restricted themselves to the nesting areas all year round, had small home ranges and were sedentary (Hutton, 1989). The data Hutton (1989) collected on large males showed non-overlapping ranges i.e. they are territorial during the breeding season (Cott, 1961; Modha, 1967; Hutton, 1984). In contrast, Kay (2004a) found that mature *Crocodylus porosus* females had a distinct and separate dry-season habitat and moved into the breeding area at the beginning of the rainy season. This difference could be related to the different nesting techniques (mound as opposed to hole) used by the above species. In Lake St. Lucia, the seasonal movement of mature crocodiles was influenced by breeding status, salinity, the presence of humans and fish migrations (Leslie, 1997). Large numbers of Nile crocodiles congregated, having covered fairly large distances, around Central Island in Lake Turkana (Kenya) for the purposes of courtship and mating (Graham, 1968; Modha, 1968).

Radio-telemetry and mark-recapture techniques (Cott, 1961; Hocutt *et al.*, 1992; Sah & Stuebing, 1996; Leslie, 1997; Swanepoel, 1999; Kay, 2004c; Campos *et al.*, 2005) are two methods used to determine crocodilian movement patterns. Radio telemetry was used to track *C. niloticus* in Lake Ngezi, Zimbabwe (Hutton, 1989; Hocutt *et al.*, 1992). Other species that have

been successfully tracked include *Alligator mississippiensis, Crocodylus acutus, C. intermedius, C. porosus, Paleosuchus trigonatus* and *Melanosuchus niger* (cited in Kay, 2004a).

The probability of seeing certain animals may depend on population density (Harris, 1986). For example: a population of animals that prefer densely vegetated habitats may be forced into more open habitats due to increasing numbers and thus be encountered more frequently. Letnic and Connors (2006) suggested that subadult male *C. porosus* avoid aggression from larger males by dispersing from preferred habitats with high crocodile densities to peripheral and less favourable habitats such as marine waters. Juvenile Nile crocodiles have also been known to leave rivers to exploit the calmer, safer and possibly more prey-abundant waters of temporary pans during the wet season (Kofron, 1993b).

Male crocodiles move further and more often than females (Webb & Messel, 1978; Kay, 2004a) and are also involved more frequently in aggressive intra-specific displays than females, lending support to the "male dispersal" hypothesis suggested by Letnic and Conners (in press, cited in Letnic and Connors, 2006). However, this response has not been quantified in other crocodilian species and Woodward and Moore (1993) advocate the assumption of equal sightability under varying population levels.

Daily movement patterns are generally determined by weather. Crocodiles are ectothermic and regulate their body temperature behaviourally, by alternately sunning themselves to warm up and then moving into water or shade to cool down. Cott (1961) and Modha (1968) observed peak basking times before and after the midday heat. Crocodiles are nocturnally aquatic (Pooley, 1982), although may be found ashore moving between habitats, or lying on banks on warm, humid evenings (Pooley, 1982). Crocodiles avoid areas where their basking sites are routinely exposed to wind and wave action (Modha, 1967; Graham, 1968; Pooley, 1982). Evenings are spent in the water, where body temperature is buffered from the cooler air temperatures and this time is used to hunt. In addition to these daily movements, crocodiles exhibit a seasonal shift in behavioural patterns, tending to spend a great deal more time under water or exposing less of their bodies to the air when it is cold (Smith, 1979) and basking more frequently during the day (Kofron, 1993b).

The effect of water level on encounter rates is well documented (Woodward & Marion, 1978; Messel *et al.*, 1981; Webb *et al.*, 1990; Ron *et al.*, 1998). Changes in water levels associated with tidal shifts or flooding regimes have a profound effect on crocodilian movement (Woodward & Marion, 1978; Messel *et al.*, 1981; Messel & Vorlicek, 1987; Games, 1990; Webb *et al.*, 1990).

Messel *et al.* (1981) found that large crocodiles that were sighted at high tide were not necessarily seen again at low tide. Wood *et al.* (1985) found that *A. mississippiensis* also dispersed during high - water seasons. Where the floodplain was narrow, with little adjacent wetland, densities were not significantly correlated with water level (Wood *et al.*, 1985). Crocodilians moved out of survey areas into the surrounding floodplains or wetlands when water levels increased and concentrated in main channels in the dry season. As the more accessible main channels were normally the areas in which surveys are conducted, this seasonal shift affected the number of crocodiles observed. Games (1990) found that crocodiles moved out of his study area in the Ume River towards Lake Kariba when water levels receded in the dry season. Ron *et al.* (1998) found that water level was the most important factor affecting the spatial distribution of *Melanosuchus niger* and *Caiman crocodylus* in the Amazon Basin, with most animals remaining in flooded forests during the rainy season and retreating to the deepest areas of lakes when forced to do so by reduced water levels during the dry season. Similar tendencies were found with *C. crocodylus* in the Pantanal (Coutinho & Campos, 1996). Woodward and Moore (1993) suggested measuring water level during surveys to isolate its effect on crocodilian counts and that surveys should be conducted at the same time every year to limit seasonal variation. Given sufficient funding, surveys should be conducted throughout the year to calibrate seasonal differences for comparative purposes, especially if seasonal movement patterns are being investigated (Combrink, 2004).

6.2.1 Determining movement patterns

I. Mark-recapture

The traditional method of collecting data on crocodile movement patterns is by means of mark-recapture techniques. These methods have been used on *C. porosus* (Webb & Messel, 1978; Magnusson, 1979a; Sah & Stuebing, 1996), *C. johnstoni* (Tucker *et al.*, 1997a; Tucker *et al.*, 1997b) and *C. niloticus* (Hutton, 1984; Kofron, 1993a; Leslie, 1997). This method is useful for smaller animals (< 1.2 m total length) that are more easily and reliably recaptured when compared to larger animals. However, a drawback is having to have the crocodiles in hand to recognize them individually.

II. Radio telemetry

Radio telemetry techniques have been used to track a number of crocodilian species throughout the world, including *A. mississippiensis* (Joanen & McNease, 1970, 1972; Rodda, 1984a; Gaby *et al.*, 1985), *C. niloticus* (Hutton, 1989; Hocutt *et al.*, 1992; Swanepoel, 1999; Botha, 2005), *C.*

porosus (Kay, 2004a, c), *C. intermedius* (Munoz & Thorbjarnarson, 2000) and *C. acutus* (Rodda, 1984b; Kushlan & Mazzotti, 1989). Transmitters are usually attached to the upright scutes of the tail, where the antennae are exposed when the crocodile is on land. Animals are then located by homing in on the signal produced by their transmitter. This method can only be used for larger animals due to the size of the transmitters. Reliable fixes can usually be obtained in open habitats and the timing of the "resightings" can be determined by the researcher, as opposed to the uncertainty of waiting to recapture the crocodile. Botha (2005) found that the attachment of transmitters to the tail scutes of crocodiles was not effective and most of the transmitters were destroyed by the crocodiles themselves or by other crocodiles. The current preferred point of attachment of transmitters is on the nuchal scutes, situated on the dorsal surface of the neck (Kay, 2004b). In this position, the transmitter is continuously exposed when the crocodile is floating or swimming.

III. GPS / GSM transmitters

These transmitters are suitable for subadult or adult crocodiles in areas where there is reliable cellular coverage and they can also store coordinates when the crocodiles are out of cellular range. Most of these units have UHF transmitters attached to them and it is possible to download stored coordinates by locating the crocodiles and downloading the coordinates using a remote receiver. This method is preferred because animals that inhabit areas with reliable cellular coverage do not have to be approached and the transmitters can be set to give as many coordinates as required. This tracking method has recently been used successfully on two adult *C. niloticus* in South Africa (Botha, 2005).

IV. Satellite transmitters

Since 2002, a number of *C. porosus* adults and subadults have been fitted with satellite transmitters and these have proved very successful in monitoring daily movement for up to 10 months. Satellite collars have also been used successfully on crocodilians in India and Nepal (www.sirtrack.com/case_study_details.asp, accessed 30 August 2007). The crocodile, once captured and fitted with the transmitter, is released and no further interference takes place. Localities of the animal can be accessed by any computer with internet access and data will continue to be generated at desired intervals for the duration of the batteries' lifetime. The disadvantage of satellite telemetry is the expense, including both the initial purchase of the unit and the daily usage fee.

6.3 MATERIALS AND METHODS

6.3.1 Study site

Located within the Republic of Botswana, the Okavango Delta (Figure 50) is the world's largest inland Delta and is also the world's largest RAMSAR site.[6] The Okavango River, which feeds the Delta, is shared by three countries—Namibia, Angola, Botswana—and has a total catchment area of more than 111 250 km^2 (Mendelsohn & el Obeid, 2004). Upon entering Botswana via Namibia, the Okavango River is channelled for the first 107 km from the Botswana/Namibia border by a set of parallel fault lines (McCarthy, 2004) and this area is known as the panhandle (Figure 51). The Okavango River eventually fans out from the panhandle to create the Okavango Delta, an alluvial fan of immense, annually flooded wetlands surrounded by the Kalahari Desert. The Okavango Delta covers an area of approximately 16 000 km^2 in the dry season and over 22 000 km^2 in the annual flooding season (Mendelsohn & el Obeid, 2004).

Figure 50. The location of Botswana in southern Africa and the panhandle region of the Okavango Delta, in which this study was undertaken.
(source: **http://www.egnu.com/maps/okavango_map.html**, accessed on 28/07/07).

[6] The RAMSAR Convention is the Convention on Wetlands of International Importance.

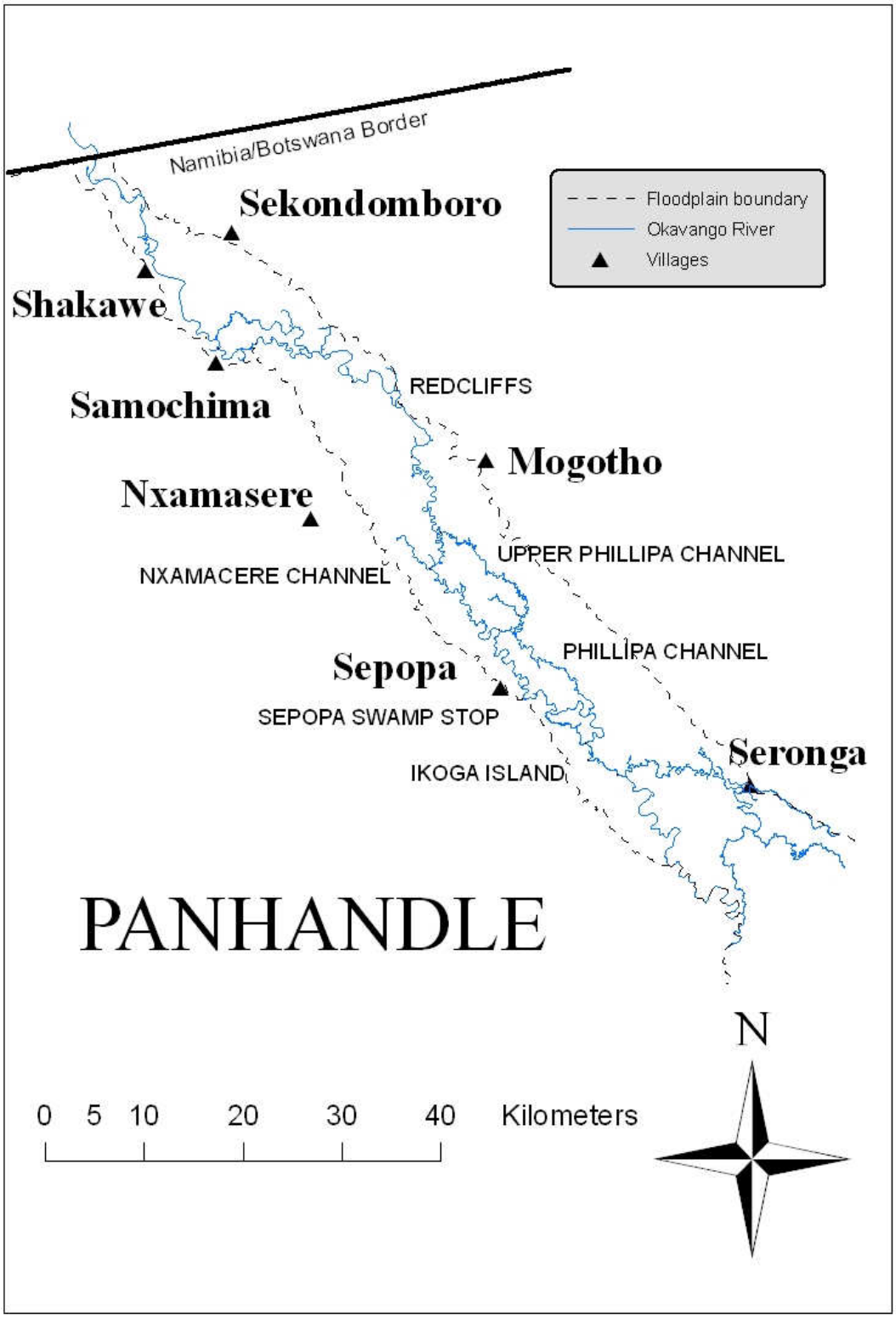

Figure 51. The panhandle region of the Okavango Delta within which the study was undertaken.

6.3.2 Capture-mark-recapture study

The CMR program was initiated in the panhandle region of the Okavango Delta in January 2002 and continued until December 2006. Nocturnal surveys were undertaken using a 5.8 m flat-bottomed aluminium boat, fitted with a 60 hp Yamaha outboard motor, and crocodiles were located and approached using a 12 volt, 500 000 candle-power spotlight (Bayliss *et al.*, 1986; Hutton & Woolhouse, 1989; Walsh, 1989; Woodward & Moore, 1993; Da Silveira *et al.*, 1997; Platt & Thorbjarnarson, 2000; Thorbjarnarson *et al.*, 2000; Brown *et al.*, 2004). Due to a reflective layer in the eye, the tapetum lucidum (Grenard, 1991), crocodilian eyes reflect any bright light shone into them and exposed crocodiles can be located for distances in excess of 100 m depending on a number of factors such as vegetation density, the strength of the spotlight and the relative position of the crocodile (Chabreck, 1966; Woodward & Marion, 1978; Hutton & Woolhouse, 1989; Combrink, 2004). Combrink (2004) provided a detailed literature review and description of the spotlight survey method. In an attempt to collect data in recapture sessions so that traditional capture-mark-recapture analyses could be conducted for this study, four blocks of time were set aside in which the entire panhandle was surveyed. This included all accessible channels from the Botswana / Namibia border near Shakawe, to Seronga, where the panhandle spreads into the Delta proper. Unfortunately, the number of recaptures obtained in these four recapture sessions was not sufficient to reliably estimate population size and so these data were incorporated into the larger, ongoing capture-mark-recapture data set.

Nocturnal spotlight and capture surveys were conducted between 20h00 and 04h00 along pre-determined, non-overlapping transects. A team of four to six boat crew members were used, including one trained observer with at least one years' intensive spotlighting experience at the front of the boat. The boat was steered along the middle of the river at an average speed of 8 – 10 $km.hr^{-1}$ with the spotlight beam traversing an arc of 180 ^{0}, illuminating river banks, the water-vegetation ecotone, and the main river channel. The observer was changed at 30 minute intervals to avoid fatigue. Water and air temperature was recorded at intervals throughout each survey period using a BATT-12 thermocouple meter (Physi-temp, CA, USA) when a crocodile was captured. When eye shine (i.e. a crocodile) was observed, crocodiles were approached slowly and quietly and captured when possible, using the size-dependent techniques described below.

1. Crocodiles up to 1000 mm in length were captured by hand, swiftly gripping them around the neck and immediately bringing them on board the boat, where they were secured by taping the jaws closed using a strong adhesive tape.

2. Crocodiles from 1000 - 2500 mm were noosed using an aluminium pole with a locking cable noose. The noose was placed over the snout and pulled tight around the neck. The animals were pulled on board the boat and physically restrained.
3. Crocodiles from 2500 - 3500 mm were noosed using a self-locking cable noose, fitted to a 3.5 m detachable pole and fastened to 25 m of climbing rope. The noose was positioned and pulled tight around the neck. These larger animals were allowed to tire themselves out before being secured and pulled on board. Animals over 3300 mm were processed on a nearby sandbank.
4. Animals larger than 3500 mm were caught using either box-traps or modified Pitman traps (see Leslie, 1997), set and baited on the river bank. These animals were noosed while in the trap or Pitman cable, and released on the rope to tire them out, before being pulled to the nearest safe river bank to be physically restrained and processed.

Animals were sampled with replacement (Underhill, 1990). Each crocodile was individually, unambiguously and permanently marked by scute clipping[20] (Figure 52). Scutes corresponding to the number assigned to the individual crocodile were removed using a surgical scalpel (Chabreck, 1963; Jennings *et al.*, 1991; Leslie, 1997; Sutherland, 2006). Crocodiles over 130 cm total length were fitted with a bright color coded and numbered plastic cattle ear tag on the most anterior single scute of the tail. These tags last for 2 - 4 years in the field. The crocodiles were sexed and blood and urine samples were taken for later analysis (part of another study), after which various morphometric measurements were recorded (see Chapter 2). The crocodiles were assigned to classes based on their size, in this case, snout-vent length (SVL), as the tails were damaged in many cases. The size classes were: hatchlings < 169 mm, yearlings 169 - 389 mm, juveniles 390 - 663 mm, subadults 664 - 1158 mm, adults >1158 mm, following those of Leslie (1997). This was necessary because it has been demonstrated that crocodiles of different sizes exhibit ecological and behavioural separation (Hutton, 1984; Games, 1990). A GPS locality was recorded at the site of each capture using a Magellan 315 GPS, in UTM / Cape datum. Crocodiles were released at, or as close to, the capture site as possible. When an animal was recaptured, its individual identity number was recorded and it was processed in an identical manner to calculate growth rates and movement patterns. Animals that were captured less than a week after being captured initially were not re-measured.

[20] The removal of certain raised caudal scutes on the tail of crocodile using a surgical scalpel, in a coded sequence, to permanently and uniquely mark the crocodile (Figure 52).

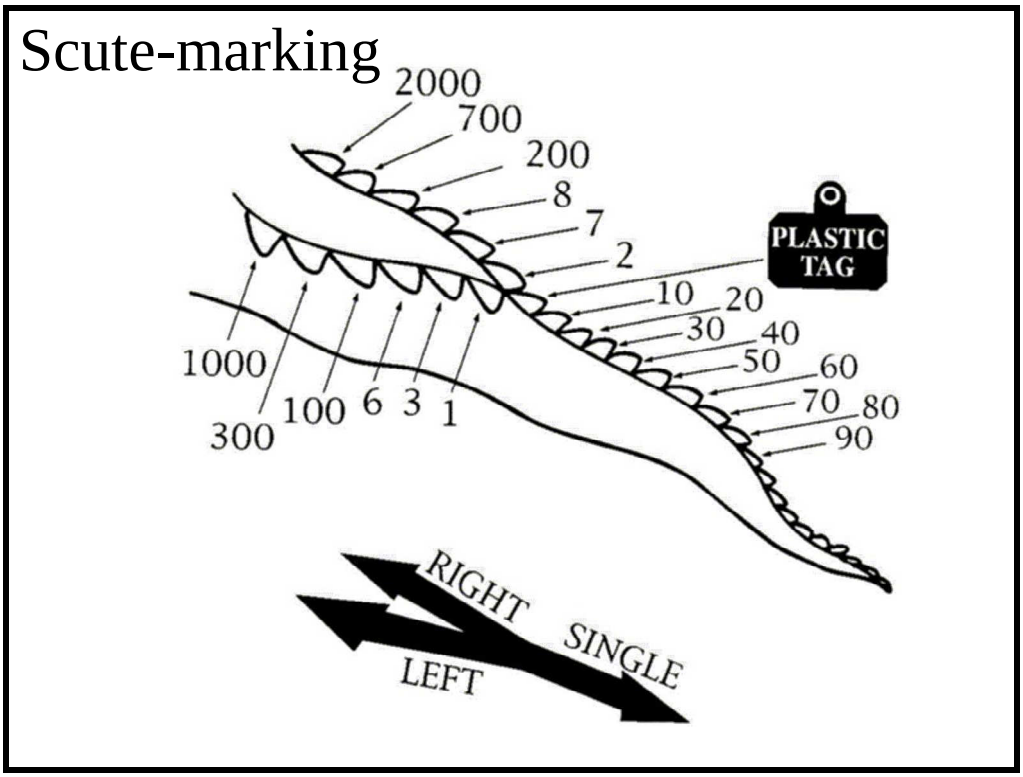

Figure 52. A diagrammatic illustration of the scute-removal method. Scutes corresponding or adding up to an individual crocodile's allocated number were removed with a sterile surgical scalpel (Leslie, 1997).

6.3.3 Radio-telemetry

As a pilot study aimed at obtaining data on the movements of larger crocodiles, a number of selected adult and subadult animals were fitted with MP2 "croc module" VHF transmitters (AVM Instrument Company, Colfax, California, USA). The transmitters were attached to the caudal scutes of the tail, in which holes were punched for cable-tie attachment. Tracking was performed on a monthly basis using a Telonics TR - 2 receiver attached to a directional 3 element Yagi antenna, operating on the 148 - 156 MHZ frequency. Although the aim of the tracking events was to actually observe the tagged animals, this was often not possible if they submerged when approached or were obscured by thick vegetation. In these instances, the closest point to the crocodiles was recorded, judging by the decibels of the received signal. This was invariably within 300 m of the animal judging by a number of tests done on the transmitters prior to attachment. These tests included submerging the transmitter until signal was lost, increasing the distance between the transmitter and receiver, and moving with the transmitter behind *Papyrus* stands. The geographic coordinates of each successfully tracked crocodile were recorded using a Magellan 315 GPS, in UTM / Cape datum.

6.3.4 Analyses

I. Mark-recapture study

The site of each capture (and recapture) was mapped using ArcGIS ArcMap v. 9 (ESRI, 2006). The distance travelled by each crocodile between captures was measured along the shortest river distance, using the measuring feature in ArcGIS ArcMap v. 9 (ESRI, 2006).

To tease out movement patterns of hatchlings, yearlings and juveniles, capture-recapture intervals were divided into the following categories: 0 - 90, 90 - 365, 365 - 720, > 720 days. The proportion of inter-capture time each crocodile spent in above average water level, water temperature and air temperature was calculated. These averages were calculated from the daily temperature data recorded during the surveys.

The average panhandle water and air temperature was calculated for 2003, 2004 and 2005, using temperature data collected at each capture site during the mark-recapture experiment using a BATT - 12 thermocouple meter (Physi-temp, CA, USA) and a Cu – Cn thermocouple probe of 1500 mm in length. Water temperature was measured approximately 400 mm below the surface, off the side of the boat. Average monthly temperatures, measured between the hours of 22h00 and 02h00, were used to standardise water and air temperatures for the duration of the project.

A sinusoidal curve was fitted to the water temperature data on a time-series scale (days since January 1, 2003) in the following form:

$$Yt = m + nt(A\cos\omega t + B\sin\omega t)$$

Where:

$$\omega = 2\pi f$$

The average number of days into the year when water temperature decreased below mean and rose above mean was calculated. The proportion of time spent in the “above average” water temperature period between capture and recapture was calculated for recaptured crocodiles.

Water level data were obtained from the Department of Water Affairs, Gaborone who recorded daily water levels (in meters) at Stations 7134 (Sepopa) and 7112 (Mohembo). The average

monthly water level was calculated from these data, and the proportion of time each crocodile spent in above-average water level between captures was calculated and explored for correlation to movement patterns. The influence of sex, water level, water temperature and air temperature on dispersal distances were examined using ranked distances (Mann-Whitney U test) because movement data displayed a non-normal distribution (Waser, 1985). A permutation test equivalent to a t-test with 10 000 bootstraps was used as a robust test of significance (Efron & Tibshirani, 1993). Maximum-liklihood Chi-squared tests were performed to investigate sex-related differences in the direction (upstream or downstream) that males and females travelled.

II. Telemetry and resightings

Subadult and adult crocodiles were extremely wary, and were almost impossible to recapture because of this. However, a number of larger crocodiles were re-sighted subsequent to capture. These were animals larger than 1.4 m total length with numbered plastic cattle tags (as described previously) When these crocodiles were re-sighted, the identification number, date and locality was recorded, plotted using ArcGIS ArcMap v. 9 (ESRI, 2006) and the distance moved since initial capture was measured.

Each discrete telemetry tracking observation was plotted and the distribution and extent of seasonal movements of the tagged animals were investigated by examining their patterns of seasonal movement using ArcGIS ArcMap v. 9 (ESRI, 2006). If crocodiles were not located for more than two consecutive tracking sessions, the panhandle was flown in a Cessna 172, fitted with telemetry tracking equipment. These flights were undertaken on two occasions, but attempts to locate the missing crocodiles were unsuccessful and we assumed that the transmitters were either damaged or lost.

6.4 RESULTS

6.4.1 Water temperature

The average water temperature over the three year period was 22.5 ^{0}C, and the sinusoidal, time-series equation to describe the best-fit line through these data was:

$$Yt = 22.85(5.53233\cos\omega t + 0.92939\sin\omega t)$$

where:

$\omega = 2\pi f$ (Figure 53).

The fitted curve, with an R^2 value of 86.2 %, intersected the average temperature line at 104 and 280 days (2003), 469 and 645 days (2004) and 834 and 1010 days (2005) after January 1, 2003 (Figure 53).

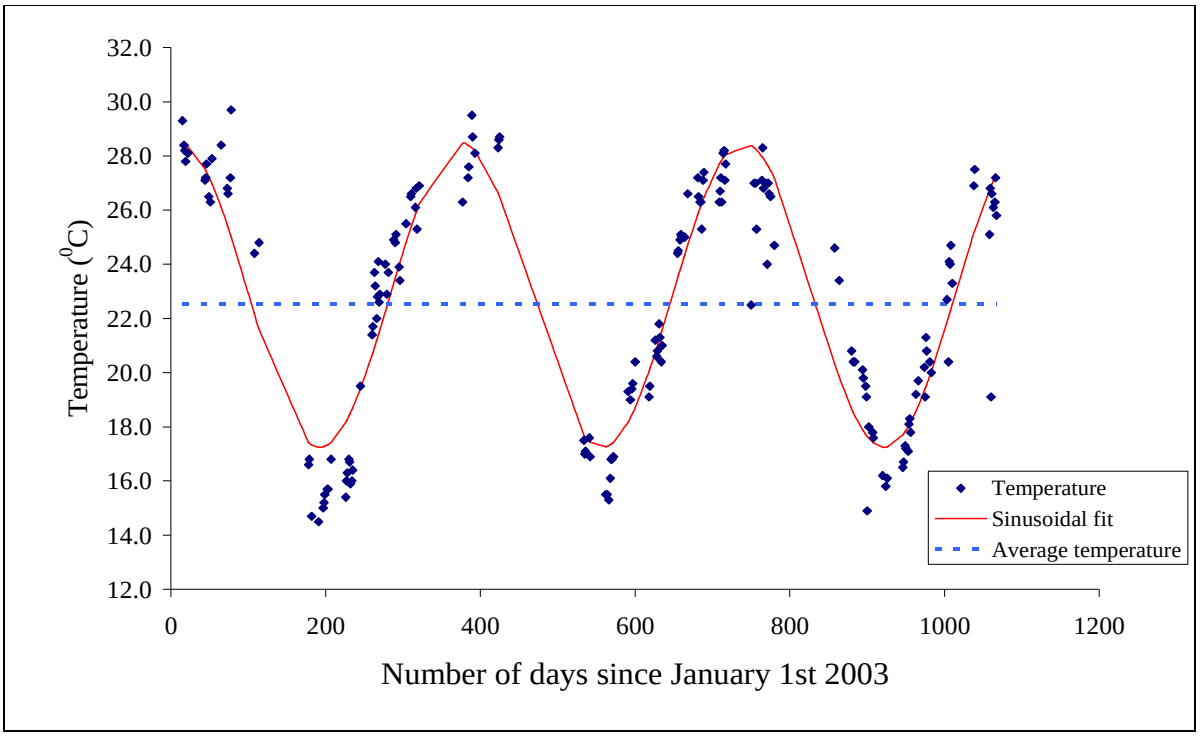

Figure 53. Sinusoidal, time-series equation to describe the best-fit line through water temperature data, recorded between the hours of 22h00 and 02h00 during night shifts, using a BATT-12 thermocouple meter (Physi-temp, CA, USA).

6.4.2 Capture-mark-recapture study

A total of 1717 individual crocodiles were captured from January 2002 to December 2006, of which 271, representing 221 individuals, were subsequently recaptured at least once. Four of these animals were hatchlings (< 170 mm SVL), 214 yearlings (170 - 389 mm SVL), 38 juveniles (390 - 663 mm SVL) and 15 subadults (664 - 1158 mm). Fifty-six percent of all crocodiles captured initially and 75 % of recaptures were yearlings. There were no significant sex-related differences between crocodiles in terms of size ($F[_{1, 269}] = 3.3315$, $p = 0.07$ Mann-Whitney U test, p=0.87) (Figure 54), or in distances travelled, either in total ($F[_{1, 269}] = 1.0917$, $p = 0.30$ Mann-Whitney U test, p=0.40) (Figure 56) or by day ($F[_{1, 269}] = 0.98658$, $p = 0.32$ Mann-Whitney U test, p=0.19) (Figure 56). The recaptures generally did not move very far: 87.9 % moved less than 5000 m from the point of initial capture, 71.7 % moved less than 1000 m and 62.5 % of animals moved less than 500 m.

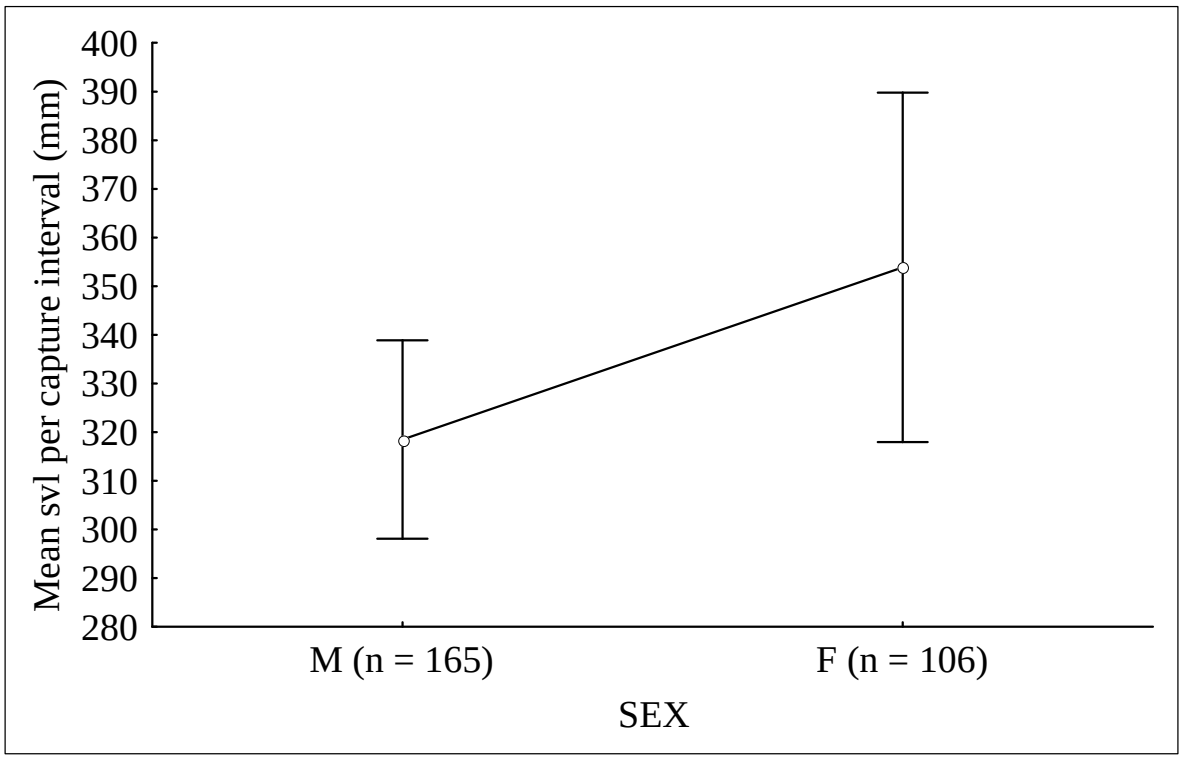

Figure 54. The mean inter-capture snout-vent length (mm ± 95 % CI) for all recaptures in the panhandle. Females were larger than males, but not significantly.

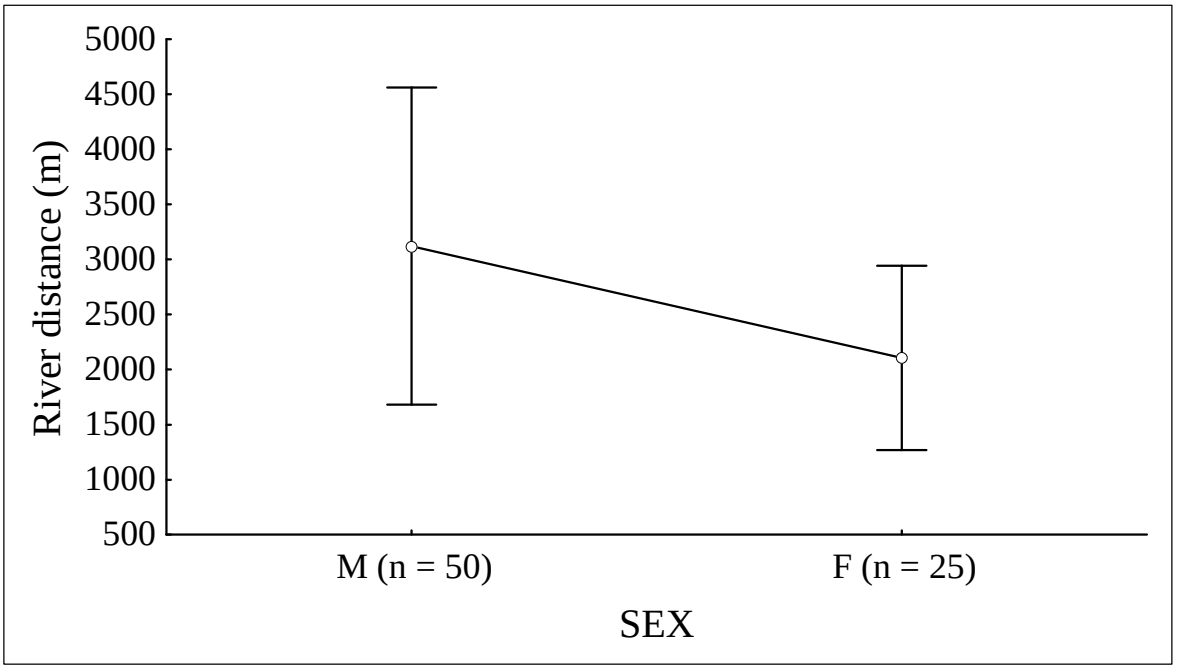

Figure 55. The average distance (m ± 95 % CI) travelled by all male and female recaptures in the inter-capture period. Males travelled an average of approximately 1000 m further than females, but this was not significant.

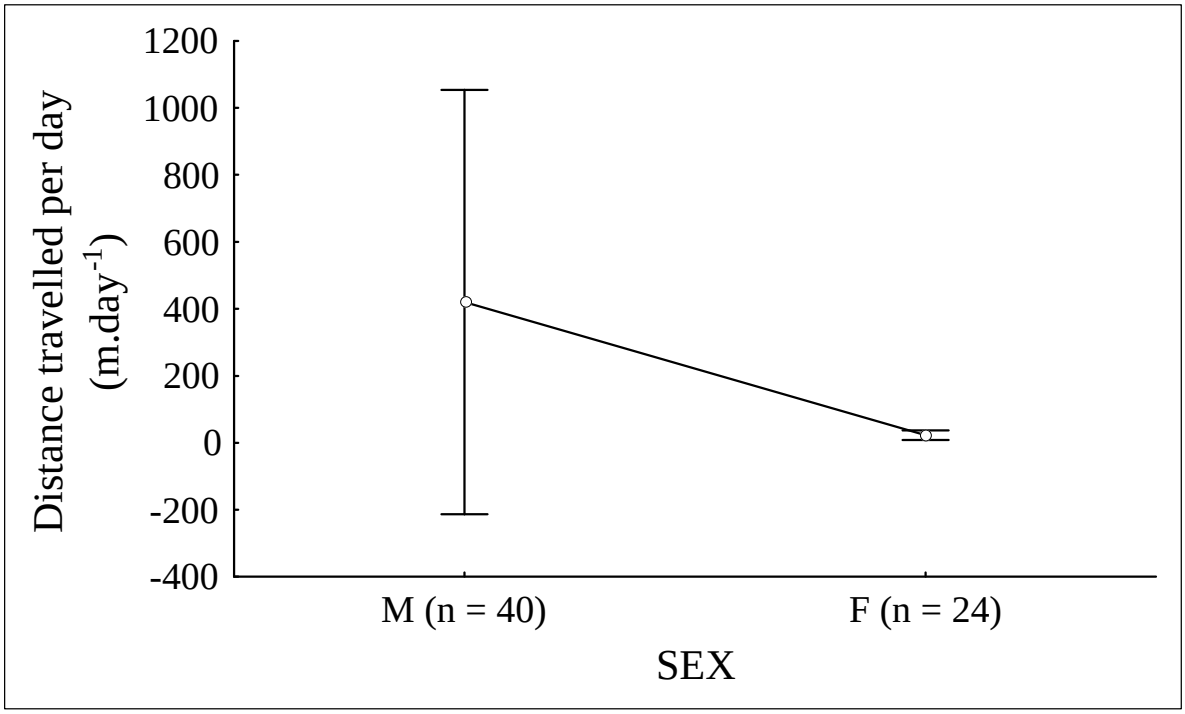

Figure 56. The average daily rate of travel ($m.day^{-1}$ ± 95 % CI) by all male and female recaptures. The wide range exhibited by males is due to a few animals that travelled much further than the majority.

There were no significant differences in the directions travelled between male and female crocodiles (maximum-likelihood Chi-squared test, p = 0.06) and although a relatively higher percentage of males moved downstream (males 65 % and females 54 %) (Figure 57), the majority of crocodiles moved with the current.

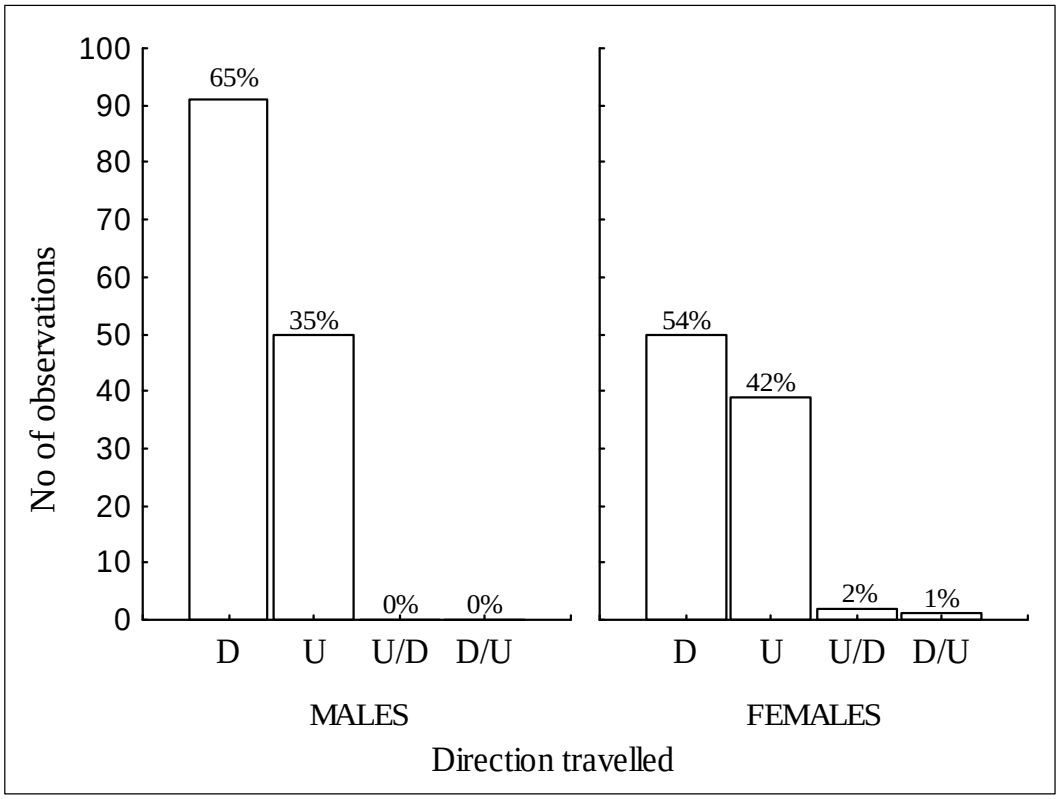

Figure 57. The direction travelled by male (M) and female (F) recaptures. The letters on the X - axis indicate direction: D = downstream, U = upstream, U/D = upstream and then downstream, usually between the main channel and a side-channel and D/U = downstream then upstream. The majority of these movements were within 500 m of the initial point of capture.

I. Hatchlings

A total of four hatchlings were recaptured. Three were captured within two weeks of initial capture and had travelled 0 m, 53 m and 387 m respectively, whereas the fourth individual was recaptured 145 days after initial capture and had covered a distance of 3 824 m.

II. Yearlings

A total of 215 yearlings, representing 170 individuals, were recaptured of which 106 were male and 64 female. This reflects a possible M:F sex ratio of 1.66:1.0.

The intervals between capture and recapture of yearlings ranged between 1 and 1143 days, with a mean inter-capture time of 158 days (median = 85 days). The mean distance (river length) travelled by yearlings between captures was 2 634 m, with a range of 0 - 52 517 m. However, this was non-representative of the data, as 61 % of yearlings moved less than 500 m and 86 % moved less than 5 000 m from the original point of capture throughout the duration of the study (Figure 58). The median value of 245 m, rather than the mean distance, was therefore a more accurate representation of the distances travelled by these crocodiles. This distance represented the minimum distance travelled as the recapture data represented a "snapshot" view of their movements. Crocodiles possibly ranged further than reported and could have been recaptured on the return leg of their journey. Crocodiles may have moved from one location to another in one journey, or broken the journey up into a series of shorter stretches to reach their destination.

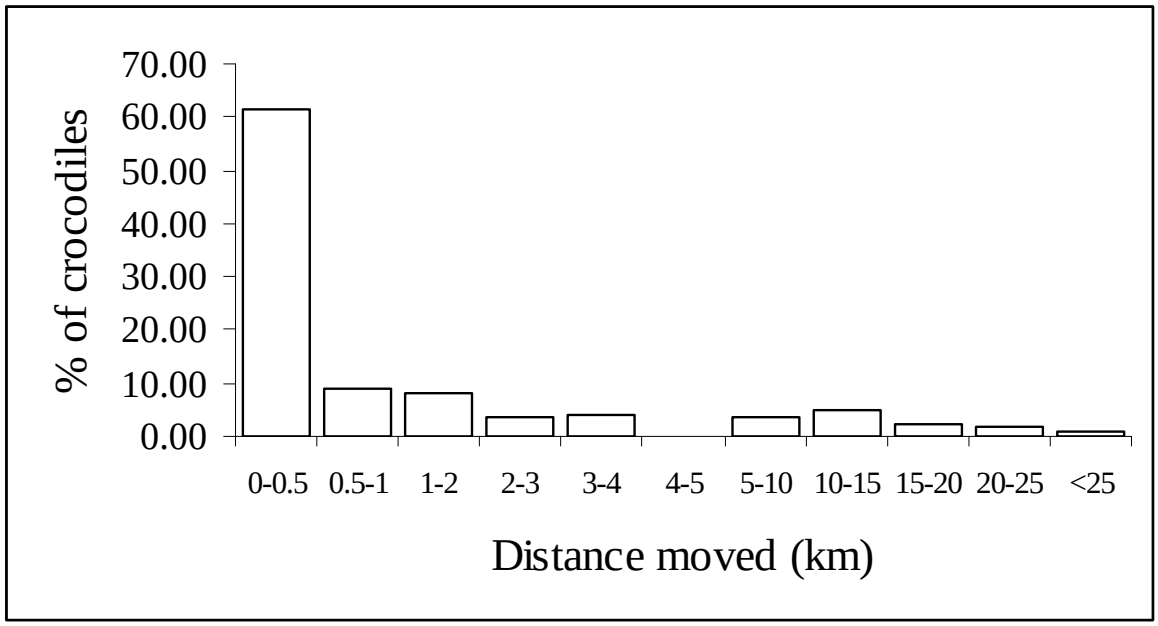

Figure 58. The minimum distances travelled by all yearlings along panhandle channels for the period between initial capture and recapture.

A. 0 - 90 days

A total of 113 yearlings were recaptured within 90 days of initial capture. Of these, 71 were male and 42 female. Males were not significantly larger than females (Mann-Whitney U test $p = 0.07$), (males SVL = 283.4 mm, females = 262.6 mm). Gender correlated significantly with distance travelled by crocodiles (SROC = -0.38, $p < 0.05$). Males travelled further than females (Mann-Whitney *U* test $p = 0.08$) and although this mean difference is just over 2000 m (males 2672.4 m

and females 569.0 m), it is not significant and probably reflects the fact that the longest distances were generally travelled by two males, with one male moving 30 000 m and another 52 571 m (Figure 59). However, median distances for males (181 m, 10.0 m.day^{-1}) and females (41 m, 1.3 m.day^{-1}) also reflected this trend. The longest distance covered by a female was 20 257 m (Figure 59) While there was a significant correlation between sex and mean SVL of yearlings (SROC = -0.19, $p < 0.05$), males and females were not found to be significantly different (K-S, $p > 0.1$). The inter-capture mean SVL for males was 282.3 mm, while the average for females was 265.4 mm.

Overall, average distance travelled per day was 112.69 m ± 55.57 (SE), with a median value of 5.91 m. This distance was correlated to the amount of time individuals spent in above average water level (SROC = -0.20, $p < 0.05$). Crocodiles travelled a greater distance as water level dropped and associated with this, had travelled further daily. In addition to this, for animals recaptured within 90 days, the distances travelled were significantly correlated to size (SROC = 0.25), with larger animals travelling further. There was no significant difference in the rate of travel (daily distance) between males and females (Mann-Whitney U test $p = 0.38$), or the direction in which they travelled (Mann-Whitney U test $p = 0.84$).

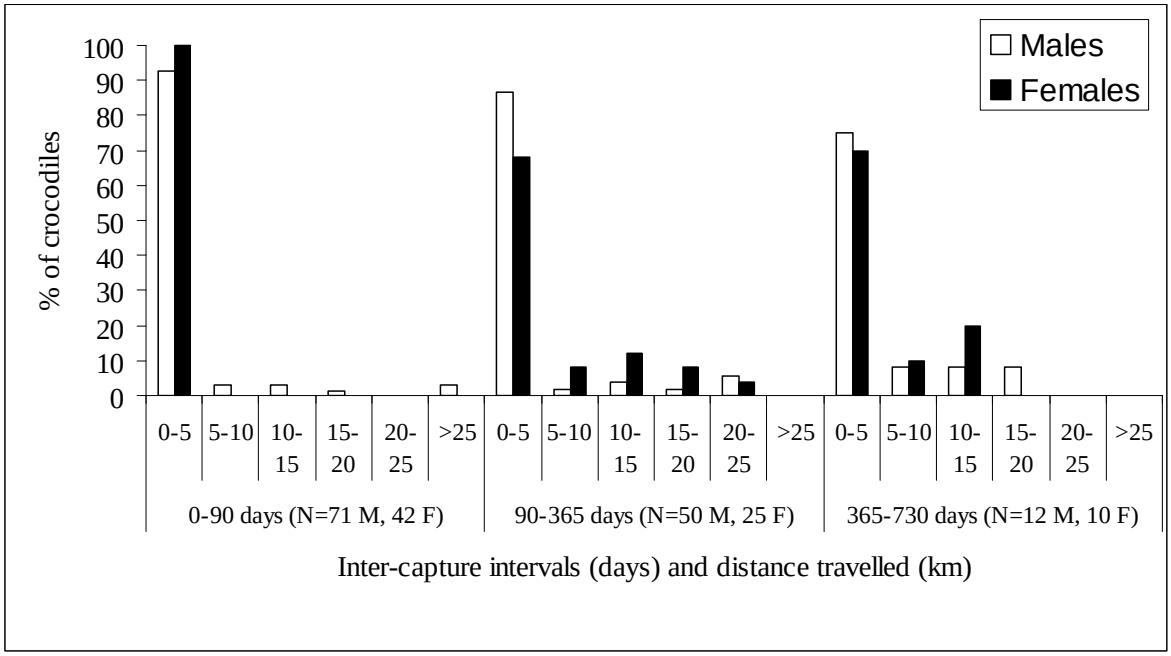

Figure 59. Distances travelled by yearlings. X-axis categories are divided into 5 km intervals and inter-capture time periods (days).

B. 90 - 365 days

A total of 75 yearlings were recaptured between 90 and 365 days after their initial capture. Of these, 50 were male and 25 were female. Males were not significantly larger than females (Mann-Whitney U test p = 0.90, males SVL = 264.2 mm ± 8.3 (SE), females = 262.4 mm ± 11.8 SE).

The average distance travelled in the inter-capture period was 3 640 m ± 737 (SE), with a median distance of 594 m. The average daily dispersal was 19.7 ± 4.49 m, with a median value of 3.78 m. Over the course of a year, both absolute distance travelled and distance per day were correlated to sex (SROC = 0.25, $p < 0.05$), with a larger percentage of female crocodiles travelling further than males (Males = 2 885.18 m ± 865 SE; median = 308 m, Females = 5 151.88 m ± 1 350 SE, median = 1 069 m, (Figure 59). However, again, few animals moved over 5 km (7 males and 8 females) and only half the number of females as males were captured.

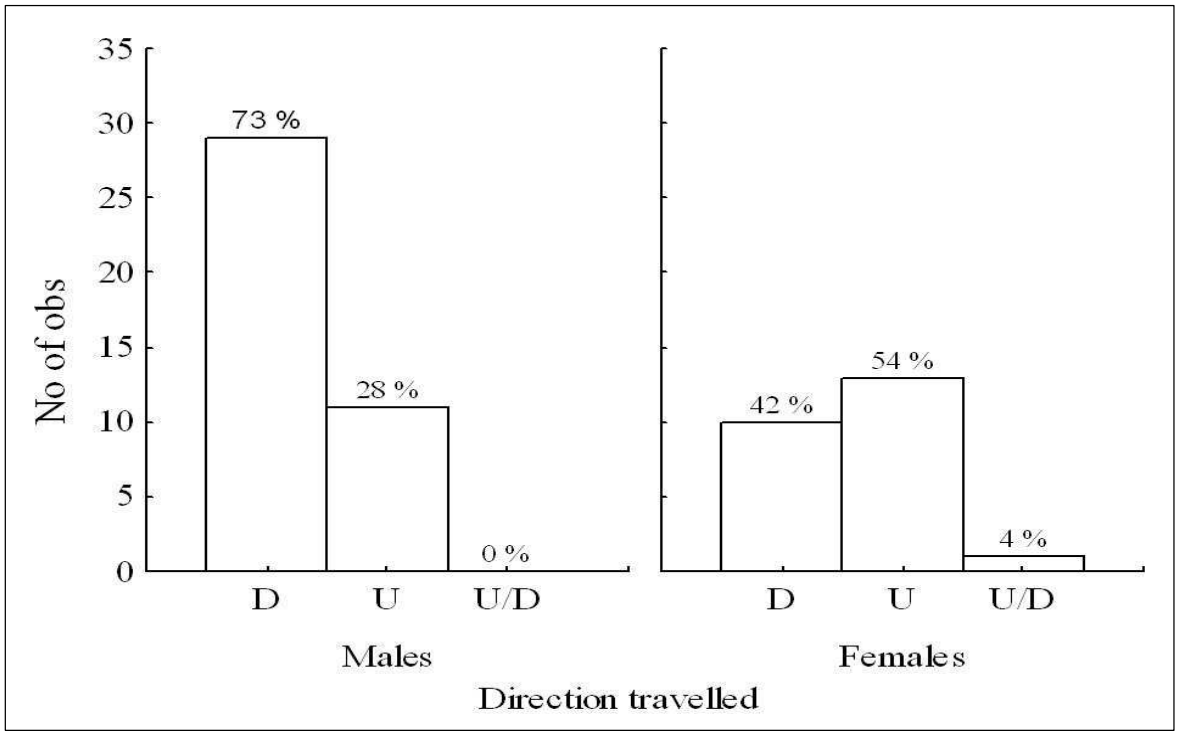

Figure 60. The direction travelled by male (M) and female (F) yearlings between 90-365 days after capture. The letters on the X-axis indicate direction; D = downstream, U = upstream, U/D = upstream and then downstream, usually between the main channel and a side-channel and D/U = downstream, then upstream. The majority of these movements were less than 500 m from the initial point of capture.

The majority of males (86.5 %) and females (68 %) moved less than 5 000 m from the point of capture and there was no significant difference between the sexes (Mann-Whitney U test $p = 0.15$). Rate of travel was not significantly different between males (15.56 $m.day^{-1}$) and females (26.0 $m.day^{-1}$). The distance travelled was not correlated with water level, water temperature or air temperature.

The majority (73 %) of males moved downstream, while significantly fewer (42 %) of females did (Maximum likelihood Chi-squared test, $p = 0.03$, Figure 60).

C. 365 - 730 days

Twenty two yearlings were captured between one and two years after initial capture, of which 12 were male and 10 female. Again, there was no significant difference in size between males and females (Mann-Whitney U test $p = 0.27$, males SVL = 319.96 mm ± 10.8 [SE], females = 300.22 mm ± 14.32 [SE]).

The mean distance travelled by these crocodiles was 4 106.77 m ± 1 072.89 (SE), with a median distance of 1 804.5 m. The mean distance per day was 10.09 m ± 2.59 (SE), with a median of 5 m. None of the recaptured crocodiles had moved more than 5 000 m from the point of initial capture (Figure 59). Male and female movements were very similar and there was no significant difference between distance travelled by male and female crocodiles (Mann-Whitney U test $p = 0.57$).

Although there was no correlation between distance moved, water temperature and water level, there was a significant correlation between distance moved and air temperature (SROC = 0.50, $p < 0.05$). Dispersal distance increased with the proportion of time spent in above average air temperatures. There was no significant difference in the direction that males and females dispersed (maximum likelihood chi-squared test $p = 0.39$), although 73 % of males and 56 % of females moved downstream.

D. > 730 days

A total of 5 yearlings (as determined by mean SVL in the inter-capture period), three males and two females were captured over three years after initial capture. Distances covered ranged from 10 - 14 207 m and there was no significant difference between male and female movement (K-S $p < 0.1$). The average daily distance travelled was 4.43 m ± 3.072 (SE). The distances covered

were positively correlated to the proportion of time spent in above average water temperature (SROC = 0.97, P < 0.05), but not air temperature or water level.

III. Juveniles

Thirty-eight recaptures were made of 35 individual crocodiles during the course of the study, of which 20 were male and 15 female. These crocodiles were recaptured between one and 1 074 days after initial capture (median = 48.5 days), covering distances between 0 - 77 903 m, with a mean distance of 3 934.18 m. ± 2 401.80 (SE) and a median distance of 102.5 m (Figure 61). The mean distance per day was 119.5 $m.day^{-1}$ ± 74.43 (SE) (0 – 2 755 m), with a median of 3.05 $m.day^{-1}$. The majority of juveniles (70 %) moved less than 1 000 m from the point of original, and 61 % of juveniles moved less than 500 m (Figure 61). The only two animals that travelled over 5 000 m were males that moved 50 792 m and 77 903 m respectively (Figure 61). The male that travelled the furthest was the only recapture that moved from the northern panhandle into the southern panhandle region. The distances travelled on the river were significantly, positively correlated to the proportion of time spent in above average water temperature (SROC = 0.18, $p < 0.05$) and air temperature (SROC = 0.18, $p < 0.05$). The rate of travel ($m.day^{-1}$) was significantly, negatively correlated to the proportion of inter-capture time spent in above average water level (SROC = -0.12, $p < 0.05$) and positively correlated to the proportion of time spent in above average air temperature (SROC = 0.12, $p < 0.05$). There were no significant differences between male and female crocodiles in terms of the distances they travelled (Mann-Whitney U test p = 0.41), or their daily rate of travel (Mann-Whitney U test p = 0.20).

A. 0 - 90 days

A total of 24 juvenile crocodiles were captured within 90 days of initial capture, 16 males and 8 females. The males moved from 0 m to 2 755 m, with an average of 468.81 m ± 200.08 (SE) and with a median distance of 102.5 m. The daily rate of travel was 244.69 $m.day^{-1}$ ± 173.66 (SE), with a median of 3.26 $m.day^{-1}$. Females moved from 0 m to 3 732 m, averaging 854.13 m ± 504.68 (SE), with a median distance of 161.5 m. The average rate ($m.day^{-1}$) of travel for females was 18.80 $m.day^{-1}$ ± 9.51 (SE), with a median of 5.6 $m.day^{-1}$. The differences between the distance or rate of travel between males and females were not significant (Mann-Whitney U test p = 0.54; 0.50).

The distances travelled did not correlate with the proportion of time spent in above average water level (SROC = -0.09, $p > 0.05$), water temperature (SROC = 0.09, $p > 0.05$), or air temperature

(SROC = 0.11, p > 0.05). There was no significant difference in the direction of movement (Maximum likelihood Chi-squared test p = 0.76), with 32 % of males and 32 % females moving downstream.

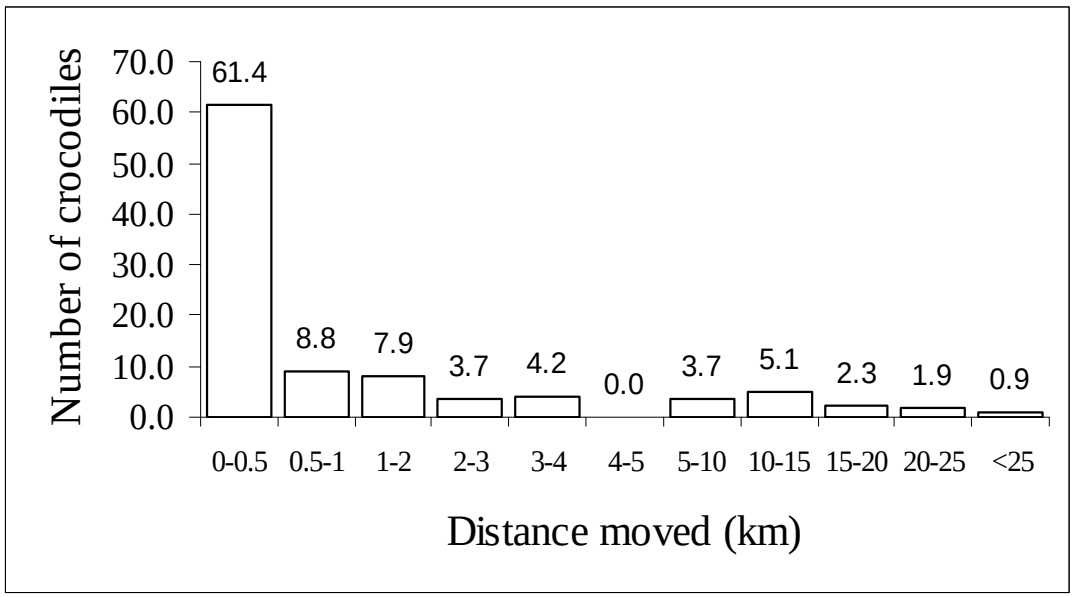

Figure 61. The minimum distances travelled by all juveniles in the panhandle region of the Okavango Delta in the inter-capture periods.

B. 90 - 365 days

Ten juveniles were captured between 90 and 365 days after initial capture, 4 males and 6 females. Males travelled between 129 m and 50 792.0 m, with a mean distance of 14 146.25 m ± 12 234.32 (SE) and a median of 28.32 m. The dispersal rate of males was 96.32 $m.day^{-1}$ ± 83.21 (SE), with a median dispersal rate of 19.67 $m.day^{-1}$. Females travelled 25 m - 354 m, averaging 94.83 m ± 52.26 (SE) and with a median distance of 46.50 m. The female rate of travel was 0.72 $m.day^{-1}$ ± 0.37 (SE), with a median of 0.34 $m.day^{-1}$.

There was a significant difference between male and female crocodiles in terms of distance travelled and the rate of travel (Mann-Whitney U test p = 0.02; 0.03), with males travelling further. Distance travelled was not correlated to the proportion of time spent in above average water level (SROC = -0.46, p > 0.05) or air temperature (SROC = 25, p > 0.05), but was significantly correlated to the proportion of time spent in above average water temperature (SROC = 0.66, p < 0.05)

C. > 365 days

Four juveniles were recaptured more than 365 days of initial capture. These animals were recaptured after 646, 736, 745 and 1 074 days, having moved 13, 28, 67 and 77 903 m respectively.

IV. Subadults

Fifteen recaptures were made of 12 individual crocodiles, of which eight were female and four were male. They were recaptured between two and 1015 days after initial capture (median = 158 days), covering distances between 14 – 8 367 m, with a mean distance of 1 169 m. ± 567.98 (SE) and a median distance of 452 m. The mean distance travelled per day was 15.6 $m.day^{-1}$ ± 6.27 (SE) (0.08 – 88 m), with a median of 3.5 $m.day^{-1}$. The distances travelled on the river were not significantly correlated to the proportion of time spent in above average water temperature (SROC = 0.16, $p > 0.05$), air temperature (SROC = 0.30, $p > 0.05$) or water level (SROC = -0.37, $p > 0.05$). There were no significant differences between male and female crocodiles in terms of the distances travelled (Mann-Whitney U test $p > 0.05$), or daily rate of travel (Mann-Whitney U test $p > 0.05$).

A. 0 – 90 days

There were eight subadult recaptures less than 90 days after initial capture, two male and six female crocodiles. The crocodiles travelled from 14 m to 1 136 m, with an average of 347.5 m ± 149.8 (SE), with a median distance of 133 m. The mean rate of travel was 23.1 $m.day^{-1}$ ± 10.91 (SE), with a median of 7.36 $m.day^{-1}$. The distances travelled did not correlate with the proportion of time spent in above average water level, water temperature, or air temperature (SROC, $p > 0.05$).

B. > 90 days

Seven subadult crocodiles were recaptured more than 90 days after initial capture, two males and five females. The crocodiles travelled from 14 m to 8 637 m, with an average of 2 108.57 m ± 1143 (SE), with a median distance of 778 m. The mean rate of travel was 7.04 $m.day^{-1}$ ± 3.86 (SE), with a median of 1.03 $m.day^{-1}$. The distances travelled and the rates of travel did not correlate with the proportion of time spent in above average water temperature or air temperature (SROC, $p > 0.05$), but did correlate with the proportion of time spent in above average water

level (SROC = -0.79, -0.93 respectively, $p < 0.05$). Thus, subadult movement was significantly increased with decreasing water level.

6.4.3 Re-sighting data

I. Subadults

Crocodile number 121, (a 1600 mm (TL) subadult female when initially captured on 11 October, 2002) was re-sighted on 2 October 2007 in the area of initial capture. A subadult male, number 237 (1860 mm TL) that was originally captured on 04 September 2005, was re-sighted on 10 October 2007, approximately 2.5 km downstream from the original capture sight.

II. Adults

An adult male crocodile captured on 21 June 2004 (# 216, 2733 mm TL at initial capture) was sighted on 2 October 2007. This animal was 19 000 m downstream from the initial capture site. Another male (# 441, 3177 mm at initial capture) was sighted on 5 November 2007, 730 days after initial capture, having moved 378 m downstream.

6.4.4 Radio telemetry

There was a rapid decrease in signal strength when *Papyrus* stands were between the transmitter and receiver and signal ceased for distances in excess of 300 m in these instances. Within 100 m of the transmitter, a signal was received from as deep as 2 m when transmitters were submerged. A total of nine animals were fitted with VHF transmitters. These included one female and one male subadult, five adult females and two adult males (Table 29). A month after fitting the transmitters, five of the nine animals could not be relocated. Two attempts were made to track these animals from the air, but these attempts also failed. The remaining four animals were two adult males (numbers 426 and 448) and two adult females (numbers 503 and 504). Male number 448 was fitted with a transmitter in February 2003 and was tracked a total of seven times until November 2003, when the signal failed. However, numerous sightings of this animal confirmed his sedentary nature. During the nine months that it was tracked and observed, this male did not move more than 300 m from the site of initial capture, approximately 2 km north-east from Sepopa village (Figure 62). Male number 426 held a linear territory that spanned a distance of approximately 5 km, spending the months of October 2002 and June 2004 in the region of Drotsky's Cabins and spending the rest of the time from October 2002 - June 2004 in a core area situated approximately 3 km downstream from Shakawe village (Figure 62) Although this

male's territory overlapped with both females 504 and 503, his range of movement between Drotsky's Cabins and 3 km downstream from Shakawe village was less than both females.

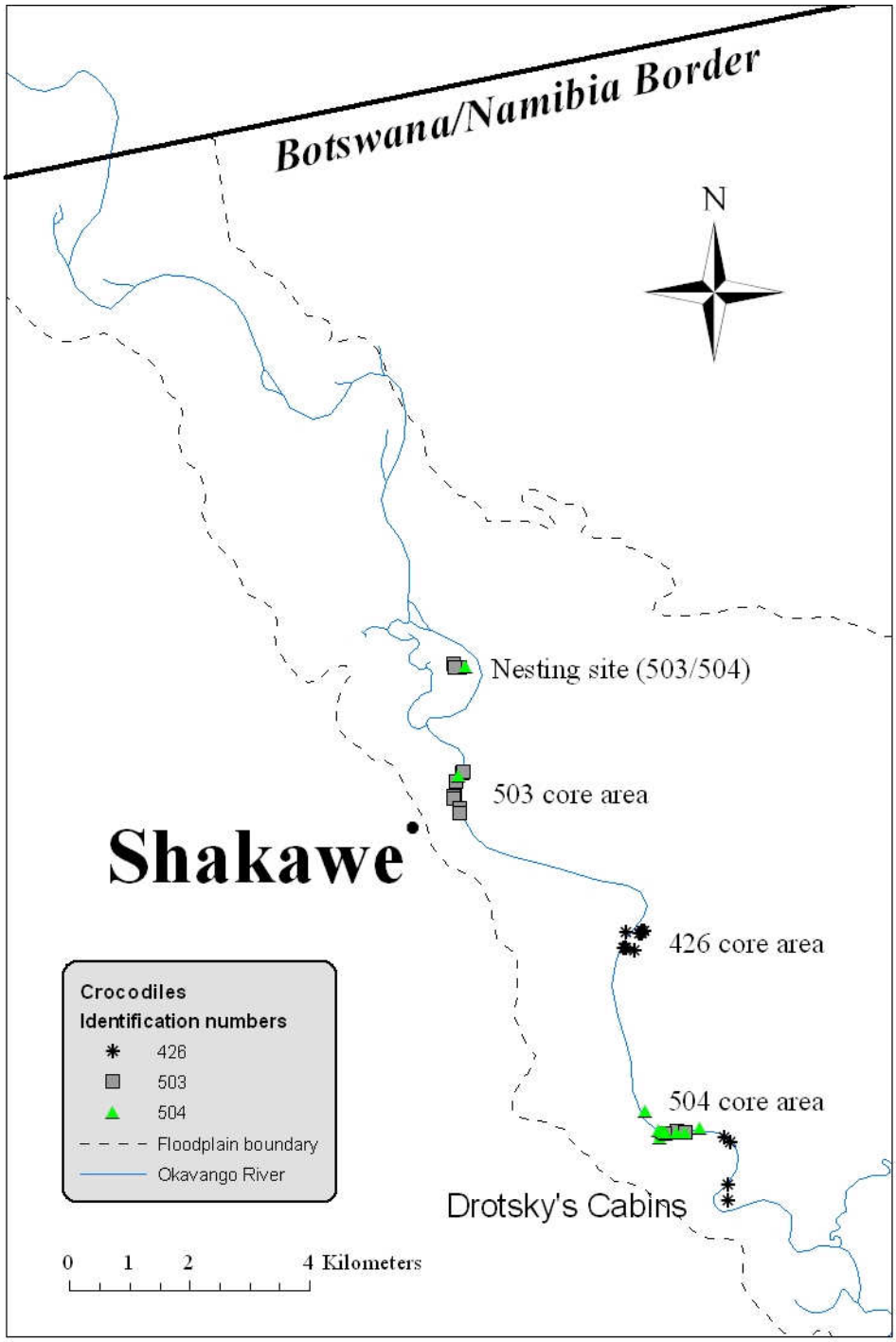

Figure 62. Localities of two tracked adult females (numbers 503 and 504) and an adult male (number 426). Each adult crocodile had an exclusive core area, but the ranges of movement overlapped.

Both females showed a range of movement that overlapped precisely and appeared to be nesting on an island north of Shakawe (Figure 62). Both females were tracked to this point during the nesting season of 2002. Although female 503 was at the nesting site on 1 October, 21 October and 14 November 2002, she was tracked to her core area, 3 km downstream from her nesting site, on 10 and 21 November 2002. This indicates that she had left her nesting site and returned to it around the 14 November. However, it was not confirmed as to whether the nests in this area were in fact these particular females' nesting sites. Female 504 occupied a core area approximately 11.3 km downstream from the assumed nesting site and 2.4 km upstream from Drotsky's Cabins. This core area signified the southern-most limit of movement for both these adult females, with the nesting site the northern-most point (Figure 62).

Table 29. Nine animals were fitted with VHF transmitters in the panhandle region of the Okavango Delta between September 2002 and February 2004. Five of the tagged crocodiles were not located again a month after being fitted with transmitters.

DATE	UTM –E	UTM –N	ID number	SEX	SVL (mm)
02/09/03	591985	7965736	504	F	1720
02/09/03	588885	7970714	503	F	1720
02/10/19	593400	7965205	426	M	2080
03/01/25	630335	7924630	348	F	1653
03/02/19	625847	7929182	448	M	2314
03/07/11	617261	7939154	350	F	1410
04/01/29	644035	7919644	358	F	1190
04/10/24	636570	7919381	366	F	1040
04/02/27	632894	7920952	48	M	973

6.5 DISCUSSION

In polygynous animals, parents maximise inclusive fitness when male offspring disperse from a defended male territory and as philopatric daughters stay near a successful female breeding area (Johnson & Gaines, 1990; Davies, 1991; Pusey & Wolf, 1996; Tucker *et al.*, 1998). Thus, a male bias in natal dispersal is predicted to result from either a greater distance travelled by males than by females, or from a higher proportion of males that move (Tucker *et al.*, 1998). Dispersal patterns are related to the reproductive behaviours of crocodilians which indicate that females select nest sites and males contest for access to these females (Tucker *et al.*, 1998). The above study concluded that the dispersal of individuals prior to reaching sexual maturity is prompted by competition for resources other than reproductive stimuli, while sexual divergence in dispersal patterns after the onset of maturity is a consequence of intrasexual competition by males for mating success.

The current study showed that, as a general rule, small crocodiles (< 664 mm SVL) did not move great distances and that there were no significant differences between the sexes. These findings are supported by a number of other studies. Hutton (1984, 1989) found that *C. niloticus* less than 2200 mm (TL) also had ranges that were small and localized and that there was no correlation between sex and movement in smaller crocodiles. Separation of juveniles from adults appeared to be ecological (Cott, 1961; Pooley, 1982; Hutton, 1989) in nature and may have resulted from the threat of cannibalism.

Tucker *et al.*, (1998), found that *C. johnstoni* dispersed at the same daily rate, regardless of sex, up to the point that sexual maturity was reached. The average rate of dispersal was less than 1000 m per year for the first 12 years. Thereafter, females did not show much movement, whereas males continued to disperse. In a mark-recapture study on juvenile *C. porosus* in Malaysia, 10 recaptured juveniles (< 850 mm TL), were within 300 m of their original capture site (Sah & Stuebing, 1996) over a median period of 19.5 days (1 - 440 days). Tucker (1987) found that the average distance moved by a sample of 153 hatchlings within their first year was 100 m. The hatchlings that were recaptured did not move large distances, although there were too few hatchling recaptures (n = 4) to be able to draw any conclusions from this study. Movement of the smaller crocodiles does correlate to some extent to yearling and juvenile movement.

Re-sighting data indicated that subadult crocodiles did not move great distances in the panhandle region of the Okavango Delta. This situation may substantiate the findings that the overall

population is currently well below carrying capacity (Chapter 2) and thus density-dependent dispersal is not a factor in the dispersal patterns within this population.

The adult males and females that were tracked showed established movement patterns, each with a definite core area. Leslie (1997) found a similar pattern from 11 adult and subadult animals that were recaptured at the site of initial capture, more than 100 days after initial capture. One adult female crocodile in Lake St. Lucia had covered a total linear distance of 8.5 km when re-sighted a year after initial capture. Another adult female that was fitted with a VHF radio transmitter patrolled a stretch of the St. Lucia estuary between the boundaries demarcating the point beyond which public access was not permitted. This female patrolled a stretch of river that was approximately 6 km long. A dominant adult male covered a distance of 17.5 km in three months, where it was seen basking with ten other crocodiles, after which it returned to the initial site of capture within the following month. Hutton (1989) found that localized home ranges were the norm for Nile crocodiles in Lake Ngezi, Zimbabwe, increasing in area with crocodile size to reach a peak in adult non-breeding females. It appears that crocodiles in the Okavango panhandle and Lake St. Lucia favoured specific basking, courtship and feeding areas (see also Hutton, 1989) and faithfully tracked these resources. A gathering of adults was observed in mid-August 2005, with densities as high as four crocodiles.km^{-1} in a stretch of the Okavango River between Nxamacere Lagoon, near Nxamacere village (Figure 51) and Christmas Island, 5 km downstream. This courtship period coincided with low - water-levels that leave the floodplains dry. Pooley (1982) also described the annual exodus of breeding *C. niloticus* from pans to nearby breeding areas along the Pongola River at the start of the breeding season. A similar increase in the number of mature animals in Lake St. Lucia, immediately following the breeding season, pointed to distinct and separate breeding and non-breeding home ranges.

6.5.1 Relocation of “problem” animals in the Okavango Delta panhandle

Crocodiles in the Okavango Delta are feared and disliked (Thomas, 2006), preying on cattle, horses, goats, dogs and occasionally humans (Thomas, 2006). Crocodiles are opportunistic and may remain in an area when food is available, becoming recognised as a “problem” animal. In many instances, the attacks on livestock go unreported, and compensation for the loss of an animal is often not claimed. Although the policy in Botswana has been the lethal control of so called “problem” animals, there has been some success in the relocation of two large male crocodiles. The first crocodile was responsible for at least one human fatality at Xakanaxa lagoon, in northern Moremi National Park, Botswana and was relocated to a crocodile farm to be incorporated into the breeding stock. Another large male crocodile was successfully relocated into the panhandle region from Xugana lagoon, in the centre of the Okavango Delta. This

crocodile remained in the panhandle region and is still seen in the area in which he was released on a fairly regular basis (Shacks, 2007 Pers. comm), presumably having set up a territory. The issue of relocation of "problem" crocodiles continues to generate debate (Webb & Messel, 1978; Walsh & Whitehead, 1993), especially in *C. porosus* populations that have recovered strongly since being afforded protection in 1971 (Webb *et al.*, 1990). Webb and Messel (1978) reported that relocated *C. porosus* have a high probability of returning to the area in which they were captured. Recently three adult *C. porosus* males that were relocated 56, 99 and 411 km (along the coastline) rapidly returned to the initial capture site after spending between 10 and 108 days at the relocation site (Read *et al.*, 2007). This demonstrated strong site fidelity, navigational skills and the ability to maintain sustained rates of travel 10 - 30 km per day in these large males. However, these populations may be approaching carrying capacity and the highly territorial nature of *C. porosus* males (Lang, 1987) may have prevented the establishment of territories at the release site, aggressively prompting these relocated animals to move back to their own territories (Messel & Vorlicek, 1986). The low population densities found in the panhandle region of the Okavango Delta (Chapter 2) would allow relocated Nile crocodiles to establish new territories at the site of release (Hocutt *et al.*, 1992). Currently the removal of any mature animals from the Delta constitutes a threat to the long-term survival of the population (Bishop *et al.*, in Press). Therefore, the relocation of problem animals to the panhandle, depending upon the nature and severity of the situation, instead of to breeding farms, is encouraged as a result of these findings.

6.5.2 Placement of transmitters

The pilot telemetry study provided data from only four of the nine adults and subadults fitted with VHF transmitters. The transmitters were attached to the caudal scutes, as close to the base of the tail as possible. In the five cases that transmitters were lost (or failed), these incidents occurred within a month of transmitter attachment. In a study in the Flagship Boshielo Dam in Gauteng, South Africa (Strauss *et al.*, 2007), 13 adult Nile crocodiles (8 male and 5 female) were fitted with the same type of transmitters used in this study. In the Boshielo Dam, study the transmitters were contained in a short length of PVC piping that was not used in the panhandle study. Additionally, two crocodiles in the Boshielo Dam study (one male and one female) were fitted with GPS / GSM transmitters, attached to the nuchal scutes of the neck. In this study, 40 % of the transmitters, including the two GPS / GSM transmitters, failed prematurely and 40 %, including all VHF transmitters, were lost. In the Kruger National Park, South Africa, 30 % of transmitters attached to the nuchal scutes of Nile crocodiles were lost within three months of attachment (Swanepoel, 1999). In contrast, in excess of 62 % of transmitters attached to the nuchal scutes of *C. porosus* adults (Kay, 2004b), remained in place and operational for 340 days

or more. As stated by Strauss *et al.* (2007), tails are targeted by conspecifics in some social interactions and as such, attachment to the tail increases the likelihood of transmitter loss. The current study therefore concurs with that of Strauss *et al.*, (2007) in advising that transmitters are not fastened to the caudal scutes of crocodilians and that the point of attachment of these devices should be on the nuchal scutes or the head.

6.6 CONCLUSION

This study supports the findings in other crocodilian studies for the size classes that were observed. Yearlings and juveniles generally did not move more than 1 - 2 km from the areas in which they were captured, while adult animals occupied very definite territories, with certain favoured core areas in which they spent the majority of their time. The establishment of sanctuary areas in the Okavango region that are free of human disturbances may assist in increasing recruitment into the population, bringing it up to carrying capacity. In addition, juveniles that originated from wild-collected eggs should be released by ranchers into low-disturbance areas. This would improve their chances of survival to maturity as they do not move great distances in the wild. Sanctuary areas would provide the ideal locations for these reintroductions.

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CHAPTER 7.

A MANAGEMENT PLAN FOR THE CONSERVATION OF THE NILE CROCODILE (*CROCODYLUS NILOTICUS*) IN THE OKAVANGO DELTA, BOTSWANA.

For submission to the Department of Wildlife and National Parks, Botswana

The format, layout and terminology of this document is based on that of "Saltwater Crocodile (*Crocodylus porosus*) and Freshwater Crocodile (*Crocodylus johnstoni*) management plan for Western Australia" (D.C.L.M., 2003), submitted under the Australian Federal Environment Protection and Biodiversity Conservation Act 1999 and the "Management Plan for *Crocodylus porosus* in the Northern Territory 2005 - 2010 (P.W.S.N.T., 2005)

7.1 INTRODUCTION

Although sporadic efforts have been made in the past to investigate the status of the population and produce a comprehensive management plan for the conservation of the Nile crocodile in Botswana, these efforts have not been effective (Graham, 1976; Simbotwe, 1988; Graham *et al*., 1992). Stewardship of the wildlife resource falls to the government through the Department of Wildlife and National Parks, which permits regulated use of it by individuals, communities and private parties (Barnes, 2001). Centralized management of wildlife in Botswana has met with limited success and there have been recent moves to entrust communities and private sectors with wildlife management and use rights at local level (Barnes, 2001).

The effective management of crocodiles in the Okavango Delta and indeed the whole of Botswana, affects all communities, at all levels. Only about one sixth of the land allocated to wildlife in Botswana has the ability to generate high economic value from wildlife utilization. This includes the land around the Okavango Delta, the northern riparian systems and some pans (Barnes, 2001). The consumptive use of wildlife, including crocodiles, bestows a monetary value on them and this value increases the likelihood that they will be conserved. Without the consumptive, economically positive use of the natural wildlife resource, livestock expansion could pose a real threat to large parts of Botswana (Simbotwe & Matlhare, 1987; Barnes, 2001). It has been demonstrated that with effective management of previously exploited crocodile populations, commercial utilization can be not only sustainable, but beneficial to the species (Webb *et al*., 1994).

7.1.1 Crocodilians and the Nile crocodile

Crocodilians exist throughout the tropics and are considered “keystone” species (Thorbjarnarson, 1992) that maintain ecosystem structure and function. These include selective predation on fish species (Cott, 1961; Pooley, 1982b), recycling of nutrients and maintenance of wet refugia in droughts (Thorbjarnarson, 1992). Three species of crocodilians occur in Africa, the slender-snouted crocodile (*Mecistops cataphractus*), the Dwarf crocodile (*Osteolaemus tetraspis*) and the Nile crocodile (*Crocodylus niloticus*). The Nile crocodile is the only one of these three species to have established itself in the eastern and southern half of the subcontinent (Blake & Jacobsen, 1992). Results of an assessment of *C. niloticus* populations in Africa revealed that populations occur in 42 African countries of which only 20 populations have been scientifically assessed (Ross, 1998; Thorbjarnarson, 1992). Since then major studies have only been carried out in South Africa (Leslie, 1997; Swanepoel, 1999; Combrink, 2004).

Crocodilians exhibit indeterminate growth and male Nile crocodiles have been known to reach 7 m in the past (Leslie, 1997) living in extreme cases to 100 years of age (Branch, 1998). Nile crocodiles are without exception the largest predators in their aquatic environments and terrestrial mammals, including humans and livestock occasionally fall victim to the larger individuals. They can tolerate a broad range of habitat types including small brackish streams, fast flowing rivers, swamps, dams and tidal lakes and estuaries (Leslie, 1997). Crocodilians are ectothermic and regulate their body temperature behaviourally, by moving between sun-exposed sandbanks and water.

Nile crocodiles exhibit a variety of vocalizations from hatchling and juvenile distress signals to adult vocalizations (in defence of young, territories, during copulation or courtship), including jaw-snapping, hissing, bubble-blowing and growling and territorial “roaring” and “bellowing” (Modha, 1967; Pooley, 1982b). Courtship displays involve a number of vocal (female only) and non-vocal (physical) displays (Modha, 1967; Pooley, 1982b). Male-male competition for mates can result in physical confrontation and the death of sub-dominant males when the ritual displays of dominant males are ignored (Pooley, 1982b). Sexual maturity is reached by females over a fairly large size range that is locality-dependent. In the Okavango region they reach sexual maturity at 232 cm total length (Detoeuf-Boulade, 2006). Breeding represents a large physiological investment on females, which may be the primary reason that wild female crocodiles only reproduce every two to three years (Graham, 1968;

Lance, 1989; Kofron, 1990; Guillette *et al.*, 1995), while farmed animals and wild dominant males may reproduce every year.

Nile crocodiles are oviparous pulse breeders that nest in summer at the end of the dry season, when sandbanks are exposed and daily temperatures are at their highest (Cott, 1961; Blomberg, 1976; Pooley, 1982b; Kofron, 1990). In Southern Africa nesting and incubation occurs between September and January (Pooley, 1982b; Hartley, 1990; Kofron, 1990). Nests are constructed in a range of substrates, from clay to course-grain, pebbled river sand. They are associated with permanent fresh water, which the attending females require to escape danger and to thermoregulate while guarding the nest (Pooley, 1982b). All crocodilian species exhibit parental care throughout incubation and a limited post-hatching time (Thorbjarnarson, 1992) often not feeding during this period. The eggs (40-80) are deposited in a nest chamber that the female excavates for this purpose, after which they are covered with sand and incubate for an average of 90 days (Cott, 1961; Graham, 1968; Pooley, 1969; Blomberg, 1976). Defense of the nest becomes aggressive when the site is approached too closely (Pooley, 1982b). Although parental care is exhibited by the female (Graham, 1968; Pooley, 1969; Blomberg, 1976; Hutton, 1984), very few of the eggs actually survive through incubation and hatching, with high (30 - 60 %) predation rates (Pooley, 1982b; Pers. obs., 2003-2006) or seasonal flooding drowning clutches. Eggs are routinely predated by the Water monitor, *Varanus niloticus* and up to 50 % of clutches may be lost to this predator alone (Trutnau & Sommerland, 2006). Only approximately 2 % of eggs laid produce hatchlings that subsequently reach sexual maturity (Pooley, 1982b). Hatchlings and young crocodiles are readily eaten by numerous terrestrial, aquatic and avian predators.

Crocodiles exhibit temperature-dependent sex determination (TSD) which means that their gender is not determined genetically. Rather, sex is determined by incubation temperature for approximately 9-10 days in the middle trimester of the 90 day incubation period (Guillette, Pers. Comm, 26 September 2007). This potentially has large-scale effects on population sex-ratios. Global warming may potentially be advancing at a rate faster than crocodiles can adapt to rising temperatures, leading directly to male-biased populations and followed by extirpation, in a worse-case scenario.

In addition to this, the increase of naturally or artificially introduced estrogens (such as DDE, thallides, phytoestrogens etc.) have been shown to lead to decreased fertility in a number of animals, including crocodiles (Guillette & Moore, 2006) and humans. Indeed, it is probable

that the early detection of altered fertility in crocodiles could be an early-warning system for similar effects in humans, who share the same water-sources.

7.1.2 Human-crocodile interaction

With the obvious and beneficial exception of ecotourism, wild crocodile / human interaction is rarely positive. Human-crocodile conflict increases with the increased encounter rates that result from rising human densities (Thomas, 2006; Combrink *et al.*, in Press) and this conflict generally results in the reduction of wild populations (Combrink, 2004). Nile crocodile populations have been drastically reduced or extirpated throughout most of their natural geographical ranges due to eradication programs or commercial hunting endeavours (Thorbjarnarson, 1992).

Disturbance caused by boat motors has a negative impact on nesting birds, mammals and reptiles that are reliant on the river for nesting sites and other resources (Mbaiwa, 2002). Mbaiwa (2002) noted that crowding of tourist facilities and noise pollution generated in these areas, negatively impacted on the river-dependent fauna and suggested that the Okavango Delta was likely to be environmentally degraded in the near future if measures were not taken to address the problem.

During the low-water season (Figure 63) fishermen and reed-cutters can easily access the floodplains. The papyrus (*Cyperus spp.*) beds lining the channels are highly combustible in the low-water season and are deliberately burnt every year at the time when female crocodiles are nesting, probably to improve access and grazing for livestock (Cassidy, 2003; Shacks, 2006). The *Papyrus* fires burn around the nest sites, often causing the attending females to abandon them. The eggs then become nest-bound due to growth of vegetation over the nest-cavities. Once abandoned, hatchlings have no assistance from attending females that would normally dig them out of the nest and carry them in the mouth to the crèche area.

At present, harming adult crocodiles may not constitute the biggest threat to the population, as it did during the periods of intensive cropping. It is clear that nesting areas in the immediate vicinity of high densities of people are exploited and have a much reduced or no chance of survival. Taylor (1973) reported that two out of 15 nests that were visited in the 1972 breeding season had the eggs removed by local people. In the 2004 / 2005 nesting season a commune of four nests was located with all eggs unearthed and destroyed near the village of Shakawe.

Crocodiles are not generally utilized by local inhabitants for their meat or hides. Thomas (2006) reported that only 1.1 % of interviewees from the Okavango Delta had consumed crocodile meat. There are persistent superstitions regarding the toxicity of various crocodile products other than eggs, such as the brain and liver (Thomas, 2006). However, eggs may be consumed when nests are located.

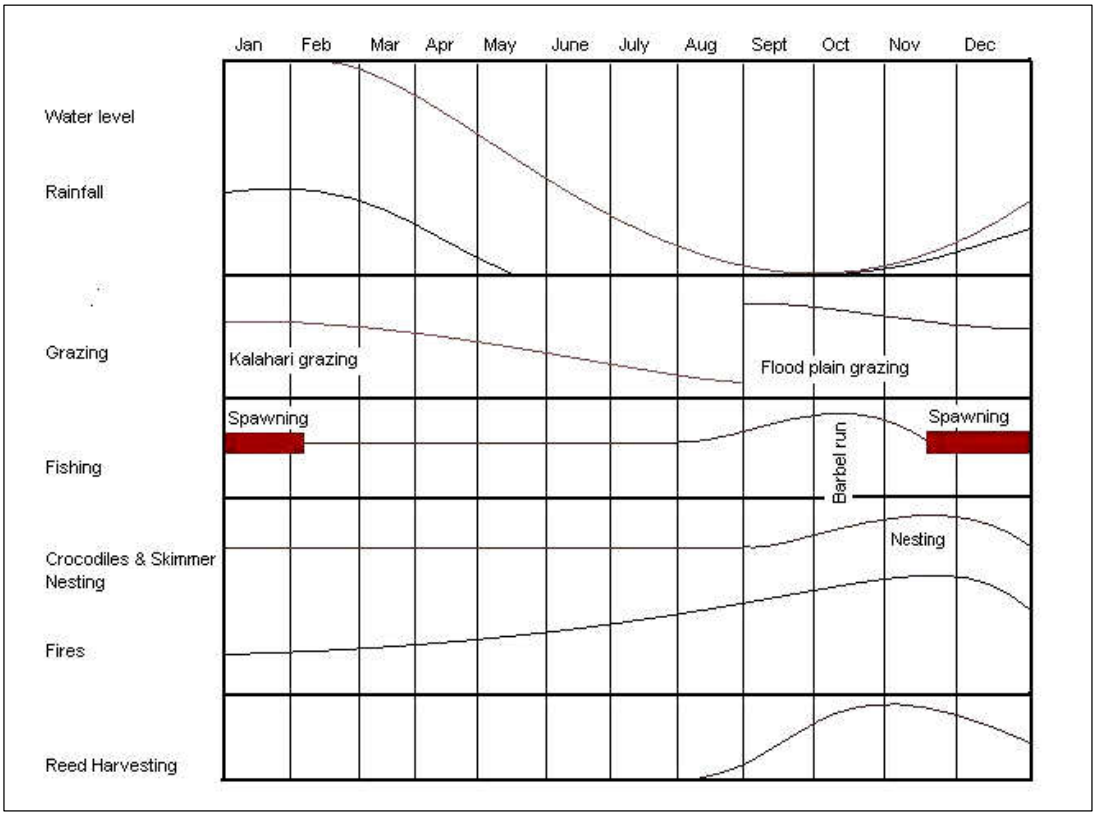

Figure 63. Various human activities in the panhandle region of the Okavango Delta showing the coincidental timing of crocodile and African skimmer nesting and fish spawning. During September and October water levels are at their lowest allowing relatively easy access into the floodplains by people and livestock (NRP, 2001).

7.1.3 The hide-hunting (cropping) and ranching trade

SUSTAINABLE USE

Since about 1970, after recognition that the uncontrolled exploitation of earlier decades had caused serious declines, many species have benefited immensely from the institution of improved protection and tightly controlled exploitation. When conservation programs have succeeded and crocodile populations have grown, problems of crocodile-human conflict often increase. Some species continue to require complete protection in protected areas and

preservation in captivity. However, the majority of the species require a more creative approach that provides incentives to people living with crocodiles to offset their real and perceived costs.
Sustainable use has become a key element in the conservation of crocodilian species An activity is sustainable if it can be continued indefinitely (IUCN/UNEP/WWF, 1991). Sustainable use is complex because we must consider both the effects on the target population (the crocodile population itself) and the effects on non-target species and the associated ecosystem (e.g. removal of crocodiles may affect wetland nutrient cycles and fish populations). In many cases, it is difficult to prove that use is sustainable, but it is relatively easy to recognize when use is not sustainable.

If people use any resource at a rate that exceeds the ability of the resource to replace itself, then the resource will become depleted.

Sustainable use of crocodilians can provide the necessary economic incentives to encourage people to maintain crocodilians and their habitats in a natural state. A general model has emerged for the successful sustainable use of crocodilians based on experience of nearly 20 years in such diverse countries as Papua New Guinea (Genolagani & Wilmot, 1990), Venezuela (Quero de Peña, 1993), Zimbabwe (Hutton & Child, 1989), USA (Joanen *et al.*, 1990) and Australia (Webb *et al.*, 1992). While each of these countries uses a different management scheme, there are elements of similarity. In each of these examples crocodilian populations have increased or remained stable in the wild while supporting economically viable levels of exploitation. This is the ultimate test of sustainability although it remains to be seen if these systems remain stable for longer time periods.

The basic components of sustainable use.
(*Points #1 and 2 were initiated in Botswana in the 1980's but it stopped there. The Okavango Crocodile research team have been working on all 9 components since 2002*).

The basic components for crocodilian sustainable use demonstrated by these programs are the following:

1. Survey: An extensive but fairly superficial survey of crocodilians was conducted using standardized techniques to establish an index of distribution and abundance. This index was compared with similar indices from other locations and through time at the same location, and general inference about the size / status of the population was made.

2. Recovery: Where necessary and indicated by the survey, exploitation was preceded by a period of complete protection. This allowed crocodile populations to increase in size and management agencies to develop expertise and infrastructure. Crocodilians have a life history strategy that enables them to recover from low population levels quite rapidly (5 - 10 years), as long as their habitats remain intact.

3. Monitoring: Based upon the same standardized techniques, a regime of periodic monitoring of the population was undertaken. Changes in the rate of exploitation were based upon the results of this monitoring program. It is noteworthy that neither survey nor monitoring need generate an absolute estimate of the number of crocodilians present, as long as a reliable index of the trend (increasing or decreasing) is obtained.

4. Biology: Exploitation of the crocodilian population was structured to focus harvest on those life stages where high mortality has the least affect on the population. This was usually the eggs and hatchlings, and adult males. Determination of which parts of a population to exploit, and how much, were derived from biological studies. The similarity of life style of different species of crocodilians has allowed the broad extrapolation of results on a few species to others with only superficial corroborating studies. It was not necessary to exhaustively study each species.

5. Caution: Levels of exploitation were kept well below the calculated levels that the population may be able to sustain. This was accomplished by implementing closed seasons, size limits, gear limitations, restricted licensing of processors and traders, harvest and export quotas, and often by the intrinsic inaccessibility of some parts of the crocodile population's range. In this way, natural environmental fluctuations and unexpected catastrophes can still be absorbed by the population.

6. Local benefit: The immediate economic benefits, and the responsibility for management were vested in the social groups closest to the extraction phase of exploitation. In Papua New Guinea these were tribal land owners, in Venezuela ranchers, in Australia and USA local businessmen and farmers.

7. Enforcement: Despite optimistic expectations that enlightened self interest would ensure good compliance with regulations, an effective enforcement mechanism was necessary to ensure compliance. This extended to harvest, trading, tanning, manufacturing and export controls.

8. Trade control: Because the main economic benefit of crocodile use is derived from international commerce, a stringent system for controlling international trade was a primary mechanism for controlling use and ensuring sustainability.

9. Economic feedback: A proportion of the economic returns from use was retained and used to support monitoring, management and enforcement. This was usually in the form of license fees, export fees, and user access charges.

Crocodilians can be used sustainably by several methods; hunting of wild crocodilians, ranching (i.e. bringing eggs or hatchlings from the wild and raising them in captivity) and captive breeding (farming) by maintaining breeding adults in captivity and raising their offspring. Each of these has advantages and disadvantages in terms of conservation value, ease of regulation, and economic costs and returns (David, 1994). Sustainability is possible and demonstrated for each method and many successful national crocodilian management systems utilize a combination of methods. Understanding the relative advantages and problems of the different methods is crucial to making sustainable use likely.

Sustainable use is the use of something associated with a process aimed at ensuring that the use can continue and that its impacts are maintained within acceptable or defined limits. The "process" refers primarily to (i) monitoring, (ii) assessment and (iii) adjustment.

It is impossible to sustain consumptive or non-consumptive uses of a wild population from simply knowing a wild population exists, unless the population itself is protected and conserved.

The Okavango Nile crocodile population has undergone three periods of human-induced decline over the last century. In 1957, the Department of Wildlife and National Parks (DWNP) allowed a quota of 2 000 animals per year to each of two concessionaries. Between 1957 and 1969 an estimated 50 000 crocodiles were shot and trapped by hide-hunters (Pooley, 1982a). It was however reported that as many as 80 000 crocodiles could have been destroyed in the Okavango delta during this time (Taylor, 1973). Taylor (1973) was informed that 40 000 skins were marketed and remarked that possibly only 50 % of animals shot were recovered. His considered opinion was that a total harvest figure of 40 000 animals was conservative.

In 1964, organized hunting ceased and in 1974 all DWNP records pertaining to crocodile hunting were lost. Actual harvest figures therefore remain unknown. In 1973 the DWNP set a quota of 500 animals per year for the Botswana Game Industries (BGI) to resume hide hunting. The quota of 500 animals was filled in 1973, but only 440 crocodiles, including only eight adults, were shot in 1974 and the venture was hereafter regarded as uneconomic and disbanded.

Between 1983 and 1998, 1053 live adults and 14 000 eggs were taken from the wild for commercial use in ranching operations. According to a nesting survey conducted in 1987 by

DWNP, this led to a 50 % reduction in the breeding population (Simbotwe & Matlhare, 1987). In 1988 the total crocodile population was estimated by aerial surveys flown along the river course to be 10 000 adults (Simbotwe, 1988). In 1987 the annual hunting quota for residents in Botswana (150 animals per year) had been reduced to 58 animals per year in response to the absence of a reliable market for crocodile products, making hunting non-lucrative (Simbotwe & Matlhare, 1987). The crocodile population in Botswana was not considered to be under threat at this time, based on previous studies which concluded that the population was stable and could easily sustain harvesting (Taylor, 1973; Blomberg, 1976).

Although the ecological carrying capacity of the Okavango Delta is unknown, all evidence points to the fact that the Delta supported a much larger population prior to commercial activities (Bishop *et al.*, in Press). The population is clearly sensitive to relatively small perturbations (Graham *et al.*, 1992) involving primarily the removal, through hide-hunting or farming activities, of wild breeding stock.

7.1.4 Scope and legislation of this management plan

This management plan addresses issues regarding the utilization of crocodiles harvested from the wild as part of ranching programs, captive breeding, trophy hunting and human-crocodile conflict. Furthermore, it includes guidelines to achieve the goals and aims listed in detail below. This management plan was prepared for the DWNP, Botswana, as the final synopsis of the research results and the presentation of management recommendations by the Okavango Crocodile Research Group, University of Stellenbosch, South Africa. These results form the culmination of five years' of comprehensive research conducted on various aspects of crocodilian ecology and physiology in the panhandle region of the Okavango Delta, Botswana.

7.1.5 Current status of the Nile crocodile

The Nile crocodile is not deemed a threatened species according to the 1996 IUCN Red list (Ross, 1998), although populations may be threatened in certain parts of its range. The intensive cropping of crocodiles has abated with the intervention of international legislation by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), which lists the Nile crocodile on Appendix II in Botswana since January 1990 (Fergusson *et al.*, 2004), Ethiopia, Kenya, Malawi, Mozambique, South Africa, Tanzania, Zambia and Zimbabwe (Ross, 1998).

7.1.6 Legislation in Botswana

There are six international treaties concerning the environment to which Botswana is a party (Maluwa, 1998):

- Convention on Wetlands of International importance especially as Waterfowl Habitat (Ramsar Convention) (1971).
- Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (1973).
- Protocol to amend the Convention on Wetlands of International Importance especially as Waterfowl Habitat (1982).
- Vienna Convention for the Protection of the Ozone Layer (1985).
- Montreal Protocol on Substances that Deplete the Ozone Layer (1987).
- Amendment to the Montreal Protocol on Substances that Deplete the Ozone Layer (1990).
- Convention on Biological Diversity (1992).

As a party to CITES since February 1978 (www.cites.org), any trade or movement in crocodiles, or animals collected from the wild, are subject to its dictates while Botswana remains a party. These dictates are stipulated in the Wildlife Conservation and National Parks Act (1992), Fifth Schedule.

TROPHY HUNTING

The Nile crocodile is designated as a game animal by the Wildlife Conservation and National Parks Act (1992). The Act establishes national parks, game reserves, sanctuaries, private game reserves, wildlife management areas and controlled hunting areas for purposes of managing and protecting Botswana's wildlife resources and relies on licensing as a strategy of control and on criminal sanctions to promote compliance. Hunting in national parks, game reserves and sanctuaries is prohibited (Maluwa, 1998), but can be carried out in wildlife management areas and controlled hunting areas only if the hunter is in possession of a hunting license or permit. Five types of license are provided for in the legislation: bird license, small game license, single game license, special game license and the Minister's license (Maluwa, 1998).

CROCODILE RANCHING

While crocodile population increases in Australia, for example, are not the result of farming or ranching per se, they were made possible by increased protection and controls on killing animals, allowing the population to increase and making commercial management possible (Thorbjarnarson, Pers. comm., 2007).

In Australia, Indo-Pacific crocodiles (*C. porosus*), have been protected since 1971 and the population of wild, non-hatchling crocodiles has increased by 50 % since farming was introduced in 1984. The population increased by 4 - 5 % per year during the 1980's and 1990's (Webb & Manolis, 1992; Webb *et al*., 1994). With strict application and enforcement of appropriate legislation, the crocodile population and all those involved (in terms of community employment, improvement of local infrastructure, improved commercial and subsistence fishing, ecotourism opportunities, etc) will benefit from crocodile ranching.

7.1.7 Goals and aims of this management plan

GOALS OF THIS MANAGEMENT PLAN:

- Secure and maintain a viable population of *C. niloticus* throughout its range in the Okavango Delta of Botswana.
- Increase public safety through education, mitigation of human-crocodile conflict and the relocation of "problem" animals, where possible
- Recommendations regarding the management of crocodiles as a sustainable resource[21] .

[21] For the purposes of this management plan, "ecological sustainability" with regard to crocodile management is encompassed by the following:

- The increase, protection and maintenance of genetic diversity, leading to viable populations of Nile crocodiles in the panhandle region of the Okavango Delta.
- Determining precautionary harvests of *C. niloticus* throughout Botswana based on temporal monitoring of population size and recruitment.
- Provision of inter-generational equity by ensuring a healthy crocodile population through the maintenance of diversity and productivity of the environment for the benefit of future generations.
- Ensuring that all decision making processes regarding the management of *C. niloticus* populations effectively integrate both long- and short-term environmental, economic and social considerations with due input from recognized scientific sources.

AIMS OF THIS MANAGEMENT PLAN

- Ensure the conservation of the *C. niloticus* population through monitoring and the promotion of research.
- Manage the population through regulation of a sustainable quota system, effective licensing and monitoring systems.
- Education on the importance and conservation of a sustainable population of *C. niloticus* at all levels in the community.

AIM 1. CONSERVATION THROUGH MONITORING AND RESEARCH

A. MONITORING

The key to the success of this management plan relies on the concept of "adaptive management". It has been shown that a fixed-harvest strategy[22] reduces population size much more rapidly than proportional harvesting and greatly increases the risk of resource depletion (Bradshaw *et al.*, 2006) because it does not provide a compensatory mechanism to accommodate environmental variation (Fryxell *et al.*, 2005). The proportional harvesting strategy requires temporal monitoring of the population to adjust harvesting quotas and forms the basis of adaptive management.

B. CURRENT RESEARCH RESULTS

These research results are the culmination of a comprehensive ecological and physiological study of Nile crocodiles undertaken by the Okavango Crocodile Research Group in the panhandle from 2002 - 2006. For further outputs from the study, see Appendix 8.

i. RECRUITMENT

The panhandle region of the Okavango Delta (Appendix 3) provides 99 % of the breeding output in the Okavango Delta (Graham *et al.*, 1992) and any decline in the suitability of this region for breeding will have catastrophic effects for the crocodile population in the Okavango Delta.

In 1987, after 76 nests had been removed by ranchers, an aerial survey recorded an additional 39 nests, giving a total of 127 nests. In the three years preceding 1987, between 175 and 350

[22] Fixed quota harvest is up to 0.2 K where K is the carrying capacity, and the population is stable and at K.

breeding females had been removed from the system, leading Graham *et al*., (1992) to estimate the total number of nests that would have been expected (without the removal of these breeding animals) at 255 nests. This was the projected number of nests based on nesting surveys in the panhandle between 1975 and 1978. Without surveys carried out between 1978 and 1988, it is probable that the number of females nesting had declined significantly by 1988 and continued to do so to the current levels. The current number of nests located by the Okavango Crocodile Research Group, with the egg-harvesting reports of Krokovango Crocodile Farm, was an average of 50 per year (49 - 54) from 2002 - 2006. This was considered a minimum as some of the nesting areas were inaccessible, but the number of nests not found was probably not more than 10 %, based on the proportion of suitable nesting habitat not surveyed. This number represents a 50 - 60 % decrease in the number of nests from that counted just 20 years ago. Human induced disturbance levels tend to be highest in the north-western panhandle, associated with high population densities, and are reduced to the south-east as channels become less accessible and the floodplain widens allowing for a decrease in human population densities.

The declining population trend, the lack of yearling animals in the northern panhandle and the absence of replacement of wild originated, ranched animals back into the system means that there is very little recruitment into the panhandle crocodile population. The probability of a population that is exposed to stochastic events being able to persist through time diminishes with population size (Bishop *et al.*, in Press). With recruitment at its current levels, it is unlikely that even the current population status will be maintained in the near future. It is essential that a proportion (5 %) of ranched animals that originated from wild-collected eggs are released back into the wild. This has not yet been done by ranchers located in the panhandle. Without the augmentation of the population from which these ranchers have been collecting eggs, the crocodile population will not survive.

ii. *BREEDING HABITAT SUITABILITY* (Shacks, 2006).

The primary aim of this study was to indicate crocodile nesting habitat vulnerability due to human disturbances to have the remaining suitable habitat protected, possibly in the form of a proposed sanctuary.

The objectives of the study were to:

- Record all nesting characteristics of crocodile nesting areas in the panhandle by carrying out thorough nesting surveys.
- Create a habitat suitability map based purely on nesting requirements and ecological criteria obtained from the nesting survey. For example: distance from water, vegetation structures, location on river, etc.
- Create a habitat disturbance map through Multi-Criteria Analyses (MCE) based on disturbance factors. For example: fire, boat traffic, human disturbance, grazing.
- Display habitat vulnerability by determining the difference between the habitat suitability map and the disturbance map, which will indicate the extent of non-disturbed or available remaining habitat in the system.
- Demarcate the remaining suitable habitat (vulnerable) for protection in the form of a proposed sanctuary.

Figure 64 shows the habitat suitability map for nesting crocodiles in the Panhandle region of the delta. The results from the habitat suitability map show that crocodile nesting habitat is plentiful in the panhandle. This fact is supported by the location of nests from the northern reaches of the study well into the southern reaches of the panhandle. The environmental factors for crocodile nesting are thus in good order along the panhandle, but the true suitability of the habitat can only be evaluated once human disturbances are factored in. Human disturbance in and around suitable habitat, changes the status of the habitat into disturbed habitat and thus unavailable habitat. The habitat suitability map created was then used in a Multi-Criteria Evaluation of habitat vulnerability. The function of the suitability map in this evaluation is to evaluate the extent of human disturbance directly on suitable crocodile habitat.

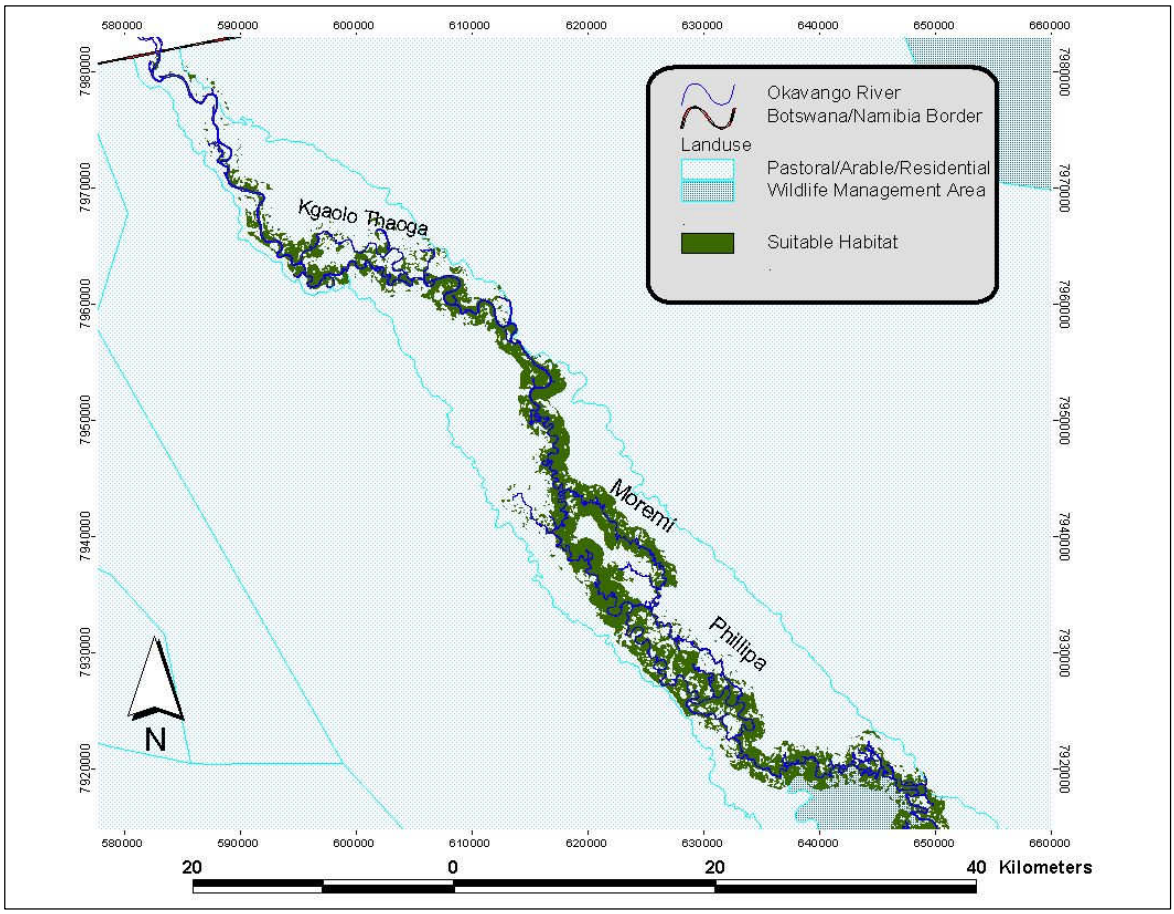

Figure 64. A habitat suitability map showing habitat suitable for crocodile nesting in the Panhandle region of the Okavango ecosystem (Shacks, 2006).

Disturbances are seen as the influence of human activities on nest site selection and nesting success. Surveys were carried out to identify areas where disturbance activities occur. For example: motor boating by tourists is known to create both noise disturbances as well as wake disturbance on nesting sites and during activities such as reed harvesting and fishing, locals are known to destroy nests as they come across them. As the nesting period coincides with the reed harvesting season and illegal burning practices in the panhandle, crocodile population figures may be severely affected. It is suspected that crocodiles abandon sites once they have been destroyed and do not return (Pers. obs. crocodile research team). Grazing by cattle is seen as another disturbance practise as domestic stock readily alter habitat quality. The crocodiles possibly thus search for other areas of suitable habitat which are further from human disturbance the following nesting season. These sites have been noted as ones which are far less accessible for reed harvesters and fisherman.

This resulting map (Figure 65) represents true habitat availability, free of any disturbances. The results of the habitat disturbance map can only be fully appreciated when compared to the original habitat suitability map (Figure 64). This comparison indicates the true spatial influence of humans on crocodile nesting habitat and clearly shows how much suitable habitat is actually jeopardized due to human disturbance. It is clear that a large amount of habitat is now no longer suitable for crocodile nesting. The exact area of both images was calculated to indicate the actual percentage of suitable habitat that is disturbed by human activities. The area of suitable habitat was 329 km², however the area of undisturbed habitat that now remains once the disturbed habitat was removed is a mere 142 km². This shows that 57 % of the projected suitable habitat is disturbed by humans leaving the remaining 43 % of the habitat as vulnerable. It is this remaining 43 % of suitable habitat that should form the basis of any protection measures in the panhandle.

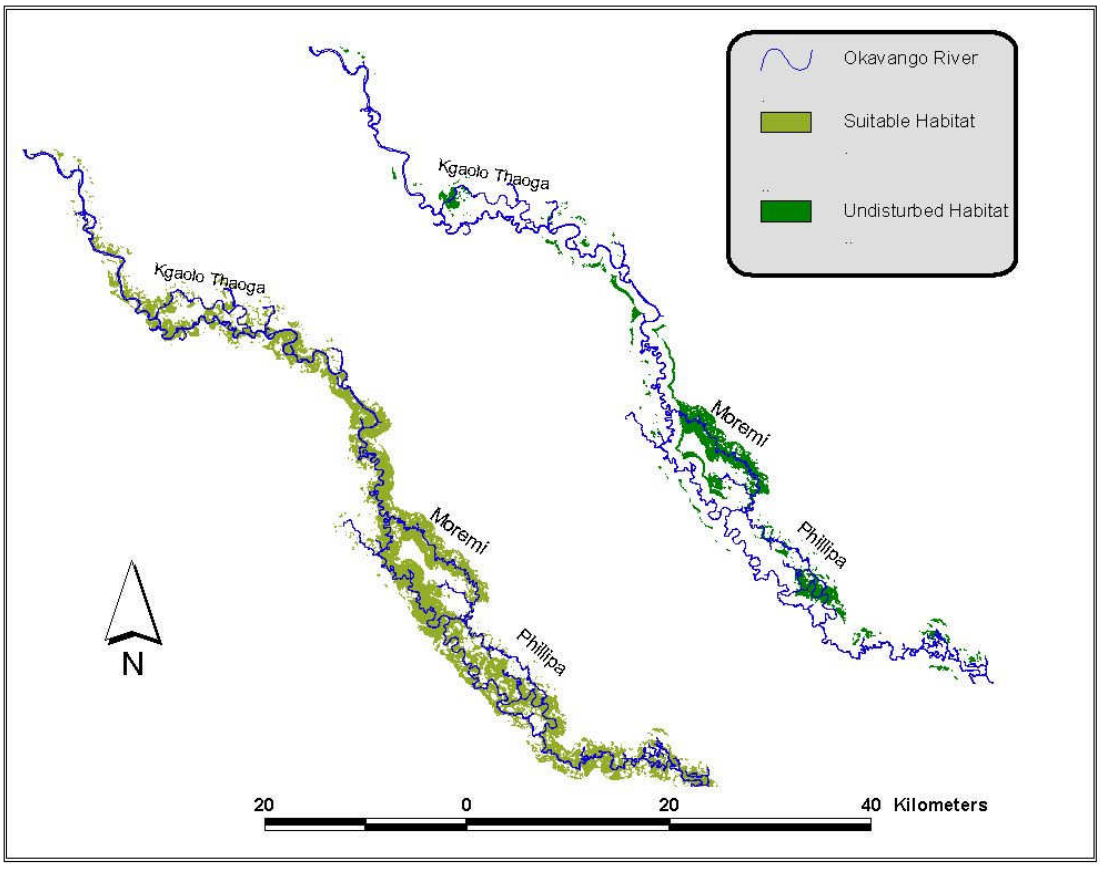

Figure 65. Habitat vulnerability. The map on the left indicates habitat suitability as shown in Figure 64. The map on the right indicates the habitat which is totally undisturbed (i.e: remaining habitat) (Shacks, 2006).

iii. DIET (Wallace, 2006).

The stomachs of 286 crocodiles (170 mm to 1660 mm snout to vent length) were lavaged (i.e. stomachs were flushed out with water) over a two year period. *Crocodylus niloticus* has a similar ontogenetic shift in diet to that of other crocodilians. Yearlings primarily predated primarily on aquatic insecta and arachnida, as crocodile size increased (juveniles, over 400 mm SVL) the diet became more diverse including crustacea, amphibia and later predominantly fish. The jaw underwent a morphological shift to cope with the new array of prey items. The largest size class in Wallace's study (sub-adults) consumed primarily fish. Yearlings fed consistently throughout the year, however a higher proportion of empty stomachs occurred within the juvenile and sub-adult size classes during the winter months. A captive experiment with wild caught crocodiles (0.7 kg – 20 kg) indicated a decrease in satiation rate (maximum mass of food eaten as a percentage of crocodile body mass) from 11.3 % to 6.5 % with an increase in crocodile size. Wild yearlings consumed 0.48 % of their body mass in prey per day and juveniles, 0.23 %. The wild conversion rates of natural prey were low, 32 % and 40 % (for yearlings and juveniles respectively) and this was possibly due to a high percentage of indigestible (chitinous) invertebrate mass in the diet. The percentage of stomach stone mass to crocodile body mass increased with crocodile size. Seven species of nematodes were found within the stomachs, four of which represent new geographic records.

Smaller Nile crocodiles feed on a wide variety of prey, being opportunistic and filling a valuable role in the ecosystem. Larger juveniles and subadult crocodiles, when feeding almost exclusively on catfish (*Clarius spp.*), possibly maintain a delicate balance between the catfish populations and commercial fish species (Cott, 1961).

iv. POPULATION ABUNDANCE

- CAPTURE-MARK-RECAPTURE ESTIMATES

The current estimate of the crocodile population in the panhandle (Bourquin, Submitted) was estimated using a combination of a Bayesian mark-recapture[23] technique and spotlight-surveys, incorporating data collected from 2002 - 2006. Animals were captured at night from a boat using a variety of size-dependent methods and trapped on the river banks using Pitman and box traps (Appendix 5). Annual population estimates were calculated for yearlings and extrapolated to the

[23] Crocodiles were marked by means of "scute clipping, the removal of certain tail scutes corresponding to the individuals identifying number (Appendix 2).

other size classes based on comprehensive spotlight-count data for size class distribution (Table 30)

Two aerial surveys were also conducted, one in the flood-season (30 June - 11 July 2005) and the other in the low-water season (5 January - 13 January 2006) to count and then estimate the total adult population (> 2.0 m) of Nile crocodiles in the panhandle region.

A total of 2679 crocodiles were encountered at night in the panhandle between June 2004 and October 2006 during nocturnal surveys, of which 456 (17 %) were “eyes only”, submerging before size estimates could be gained. Of the animals for which size estimates were obtained, a total of 18 were hatchlings (0.7 %), 714 yearlings (26.7 %), 431 juveniles (16.1 %), 417 subadults (16 %) and 643 adults (24 %). Hatchlings were not included in any further density-based analyses as too few were encountered. Overall, the crocodile encounter rate increased during the months when water levels were low (Spearman’s Rank Order Correlation = 0.67, $p < 0.05$) and were highest between September and February.

A total of 1717 individual crocodiles were captured from January 2002 to December 2006, of which 224 (13 %) were subsequently recaptured at least once. Of these, 56 % of the animals captured and 75 % of recaptures were yearlings. Yearlings constituted approximately one-third of the total population, while adult crocodiles made up approximately 25 % of the population (Table 30).

Aerial surveys

The panhandle was divided into 19 sample blocks, each 1.2 km in width and running east-west across the floodplain (Appendix 2) representing 30 % of the panhandle. A total flying time of 35 hours was required to complete both surveys and 105 and 144 adult Nile crocodiles were counted in the 2005 and 2006 surveys respectively, in a total sample area of 331.2 km2. This yielded an estimate of 380 ± 22 % adult crocodiles in the 2005 survey with an average density 0.34 ± 0.23 animals/km2 and 521 ± 17 % (95 % CI) with an average density 0.44 ± 0.23 animals/km2 for the 2006 survey. A t-test for dependent samples did not show a significant difference between the two surveys ($p > 0.05$).

The harmonic mean of the annual number of adults estimated for 2003 - 2006 was 649.2 individuals.

The sex-ratio was slightly female biased (56 % female: 44 % male) and the estimate of mature females in the panhandle, calculated from the sex-ratio, was 364 individuals. Females do not breed every year in the wild. In fact, 60 % (n = 218) were found to sexually active in a given year (Detoeuf-Boulade, 2006) and only 14 % - 23 % of these sexually active females were breeding during the course of this study. It was found through spotlight surveys that there was a significant decrease in the density of crocodiles encountered from 2004 - 2006 in the panhandle region of the Okavango delta. The total density of observed animals was negatively correlated with time (in years), with a regression equation of:

ln (Density of crocodiles) = - 0.13 (Month) + 0.57 (SE = 0.22, n = 30, R = 0.41, p = 0.03, Figure 66).

Table 30. Size-class distribution based on all eye-shine encounters (spotlight observations) from 2004 - 2006, and population estimates for other cohorts from the extrapolation of these data for the whole panhandle.

	Year	Hatchlings	Yearlings	Juveniles	Sub-adults	Adults
Size-class distribution (%)	2003*	0.90	33.4	21.2	19.2	25.4
	2004	0.75	29.0	22.5	21.8	26.0
	2005	1.65	40.4	17.7	15.6	24.7
	2006	0.29	30.7	23.3	20.4	25.4
Total estimated number per size-class	2003*	21	782	497	451	595
	2004	20	776	602	582	696
	2005	43	1061	466	410	649
	2006	8	806	613	535	667

- AERIAL SURVEYS

The panhandle was divided into 19 sample blocks, each 1.2 km in width and running east-west across the floodplain (Appendix 2) representing 30 % of the panhandle. A total flying time of 35 hours was required to complete both surveys and 105 and 144 adult Nile crocodiles were counted in the 2005 and 2006 surveys respectively, in a total sample area of 331.2 km^2. This yielded an estimate of 380 ± 22 % adult crocodiles in the 2005 survey with an average density 0.34 ± 0.23 animals/km^2 and 521 ± 17 % (95 % CI) with an average density 0.44 ± 0.23 animals/km^2 for the 2006 survey. A t-test for dependent samples did not show a significant difference between the two surveys ($p > 0.05$).

- SPOTLIGHT SURVEYS

Spotlight surveys detected 13.3 % of all crocodiles present in the low-water season and 22.4 % of crocodiles present in the high-water season. Thus, correction factors were calculated as 7.49 and 4.46 respectively for these seasons (Table 31), using the annual mean number of animals estimated by means of the mark-recapture study (n = 2621) as a total population size.

Table 31. Spotlight counts compared with mark-recapture estimates for all size classes combined, with resultant correction factors for high- and low- water periods. Crocodiles were more concentrated in the main, accessible channels during the low-water seasons.

Season	Spotlight counts		Mark-recapture estimate	Spotlight counts	Correction factor
	Average density	Total estimate	Total number of crocodiles	% of animals observed	
Low - water (September to January)	1.94	588	2621	22.4	4.5
High - water (February to August)	1.154	350	2621	13.3	7.5

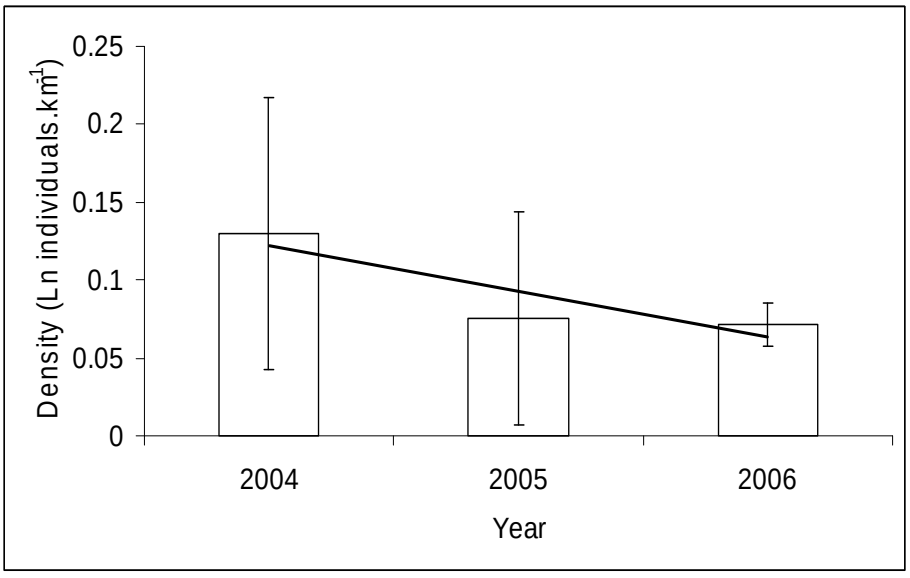

Figure 66. Graphical representation of the *ln*-transformed number of crocodiles encountered during spotlight surveys in 2004, 2005 and 2006, showing a significant decrease in numbers with time.

- CORRECTION FACTORS FOR ADULT CROCODILE COUNTS: SPOTLIGHT SURVEYS AND AERIAL SURVEYS

Spotlight surveys counted 13.3 % and 22.4 % of the adults in the high- and low - water periods respectively, and correction factors were therefore 5.0 and 7.5. The percentage of crocodiles counted during the aerial surveys was 56.7 % (low - water) and 77.7 % (high - water) of the adults estimated from the spotlight counts. Thus, correction factors for the aerial survey were calculated as 1.77 (high - water) and 1.28 (low - water).

v. THE CONSERVATION GENETICS CONSEQUENCES OF OVEREXPLOITATION IN THE PANHANDLE POPULATION

Small, isolated populations face a much higher risk of drastic reduction or extinction through stochastic processes as they are not usually as buffered by allelic diversity or heterozygosity as a larger population would be against the effects of genetic drift or selection (Frankham, 2002). It is therefore necessary to monitor the levels of genetic diversity within a threatened population. The removal of eggs and adults from this already overexploited population, without the release back into the wild or immigration of new animals, has potentially dire consequences for the population in this system. In a study investigating the effective population size of the panhandle crocodile population, it was found that moderate levels of heterozygosity had been maintained through the periods of exploitation, despite the specific targeting of adults (Bishop *et al.*, in Press). Bishop *et al.*, (in Press) suggested that the longevity and delayed sexual maturity of Nile crocodiles may have acted to buffer the expected effects of hide-hunting and the removal of breeders for farming purposes (i.e. reduced heterozygosity). However during this period, the effective population size (N_e) of the panhandle crocodiles has been reduced five-fold. Parental generation N_e has decreased from ~ 480 individuals to a current estimate of ~ 90 individuals for this generation (Bishop *et al.*, in Press). This result suggested an increased susceptibility for this population in terms of continuing decline as a function of genetic drift and selection, which results from low population size rather than a lack of heterozygosity (Bishop *et al.*, in Press). At the current effective population size, allelic diversity and heterozygosity will continue to decline through time, due to the effects of genetic drift (Bishop *et al.*, in Press). The minimum N_e required to maintain sufficient genetic variation to allow a population to persist through stochastic events varies between species, depending on their life-histories (Bishop *et al.*, in Press). It is generally accepted that maintaining > 90 % of allelic variation will ensure a populations

persistence (Spielman *et al.*, 2004). Therefore, to maintain > 90 % of the current allelic diversity and heterogeneity over the next 100 years, it was suggested that an effective (stable) population of at least 150 animals would be required. This equates to a total population of 4200 animals and an adult population of approximately 1060 individuals (Bishop *et al.*, in Press).

vi. TEMPERATURE-DEPENDENT SEX DETERMINATION

With animals that exhibit temperature-dependent sex determination (TSD) such as Nile crocodiles, climate change can potentially have catastrophic effects on hatchling survival rates, population sex ratios and thus population dynamics of a closed population such as that in the Okavango Delta. The incubation temperature of the clutch does not only affect gender. It also affects the probability that embryos will survive to hatching, growth rates before and after hatching and the probability of hatchlings surviving to two years of age (Hutton, 1987; Webb & Cooper-Preston, 1989). The selective advantage of TSD is that it assigns maleness to embryos with high probabilities of surviving and good potential for post-hatching growth (Webb & Cooper-Preston, 1989). Males are produced from clutches in the Okavango panhandle when the average incubation temperature in the middle trimester is between 31.4 ^{0}C and 33.4 ^{0}C (Maciejewski, 2006). Although reptiles exhibiting TSD have previously survived global climate change (Nelson *et al.*, 2004), these changes have occurred over long periods of time and survival has been dependent on the species being able to track the climate change to remain in tropical or sub-tropical environments. Over the past 100 years, global warming has increased by an unprecedented 0.6 ^{0}C and is projected to continue to rise at a rapid rate (Root *et al.*, 2003). In a study of 143 species of animals, more than 80 % that showed changes that were shifting in the direction expected on the basis of the known physiological constraints of the species (Root *et al.*, 2003). However, it may be that the rate of increase of global temperature far out paces the ability of crocodiles to physiologically adapt to them, or to track these changes.

vii. HUMAN-CROCODILE CONFLICT

There is significant human-crocodile conflict in the Okavango Delta and 76.3 % of people interviewed (Thomas, 2006) had a very negative attitude (fear, dislike or hate) towards crocodiles. Crocodiles are seen as competitors for fish and predators of livestock and people. There have been a total of 72 reported attacks on people since 1985 (Thomas, 2006), with the number of attacks increasing linearly since 1994, especially in 2001 (8 attacks) and 2003 (10

attacks). An overall figure of 125 individual attacks on humans, of which 55 % were fatal, was recorded by Thomas (2006) from the Delta. It was also apparent that 45 % of attacks were not reported to the relevant authorities and when these instances were reported, very often (94 % of the time) nothing was done about the report. The number of attacks correlates significantly with an increase in human density in the Ngamiland area and the highest attack incidences coincided with areas where villages were close to the river, such as Mohembo west (11), Jao (10), Samochima and Seronga (8), Mohembo East and Gumare (7). The main activities that people were engaged in when attacked were obviously all water-related, namely fishing, swimming and collecting water. The same patterns were evident with livestock attacks which had reached a peak in 2003 / 2004. Since 1941, there had been 1 703 attacks on livestock, of which 1 580 were fatal (Thomas, 2006). This total included 632 cattle, 524 goats and 231 dogs and with donkeys, horses and chickens making up the difference.

C. Future monitoring and research

Annual nesting surveys, spotlight surveys and mark-recapture surveys are ideally required, using experienced or trained persons, to monitor this population. These surveys must take place between August and December, when nesting occurs and the crocodile encounter rate during nocturnal surveys is at its highest, corresponding to the decreased water levels and increased water and air temperatures.

Yearlings provide the “best” yield in terms of mark-recapture surveys and, provided accurate size-class distribution data are obtained, can be used to monitor population health. However, this will not be applicable to the northern panhandle region, where egg-harvesting and annual releases (see Aim 2B) will influence size-class distribution patterns. It is therefore suggested that, initially, boat-based nocturnal mark-recapture surveys are concentrated in the southern panhandle, downstream from the upper entrance to the Upper Phillipa channel (Appendix 3), with periodic spotlight surveys in the northern panhandle. The southern half of the panhandle is less disturbed than the northern panhandle due to the lower human densities and will form a basis with which to compare the northern panhandle. The surveys must take place along predetermined transects and be repeated a minimum of four times per annum (August, September, October, November) to assess and account for any variability in the counts and to obtain recaptures. Once accurate correction factors can be validated for the spotlight surveys, these can be conducted on an annual basis, without the benefit of mark-recapture methods.

All crocodiles encountered must be recorded, with size estimates, to gauge current size-class distribution and those that do not submerge should be captured, sexed, weighed, measured (Appendix 7) and individually marked by means of scute clipping (Appendix 4), or preferably with the insertion of PIT (Passive Integrated Transponder) tags, to assess survival rates, growth rates, movement patterns, survivorship and overall abundance estimates.

Blood and urine can be collected from adults to monitor reproductive cycles, fertility, etc..

Nesting surveys should be conducted on foot and by boat annually during September and October. All potential nesting sites should be revisited to determine the fate of the clutches. In years that eggs are collected, the ranchers' egg harvesting reports, which must be formalised and standardised, will be used to obtain accurate data on nests numbers.

Aerial surveys should be flown to strengthen the confidence in any adult estimates and account for adults that are in areas not accessible by boat. These surveys must be flown annually in September or October to take advantage of the low - water levels.

AIM 2. QUOTA SETTING

The objective of quota setting is to ensure that the *C. niloticus* resource is used responsibly and sustainably by determining the number of crocodiles taken for commercial harvest through a best practice system that takes into account the conservation status of the population, based on continued monitoring.

A. TROPHY HUNTING

At present an annual quota of 50 trophies or live wild crocodiles may be exported from Botswana (CITES, 2007). However, in the light of the current population status, it is suggested that this quota is dramatically reduced, or suspended pending further research.

B. CROCODILE RANCHING

No breeding animals should be removed from the Okavango system until it can be demonstrated that the population is showing a positive rate of increase. These trends will be apparent within a period of six years (half a generation time) from the implementation of this management plan (Stirrat *et al.*, 2001). The exception to this will be in the case of animals

that pose a threat to human safety or primary production (i.e. livestock). These may be removed from the wild under the provisions of a license issued by DWNP and provided to licensed crocodile farms for commercial purposes, or relocated. As a condition of commercial farm licenses, it is suggested that licensees are required to accept any and all problem *C. niloticus*, as stipulated by DWNP and subject to such conditions as DWNP may impose with respect to the use of those animals for breeding or slaughter for commercial use.

Animals removed in this manner should not be considered as part of the commercial harvest quota (when such a quota is issued) and may be removed from any areas in which they pose a threat.

Provided that crocodile ranchers release 5 % of all animals originating from wild-collected eggs, annual harvesting of all nests lying outside protected "sanctuary areas" should be permitted. As an incentive for ranching practices to continue, it is suggested that eggs are freely available from the wild to licensed crocodile ranchers.

It is suggested that a maximum of 25 clutches are allowed to be removed from the system annually from outside of protected areas only until such a time as the Krokovango crocodile farm's breeding stock begin producing eggs. Twenty-five clutches currently represent 50 % of the annual number of clutches found within the panhandle and falls within the range of expected predation rates, and with a release of 5 % of this stock back into the wild, will increase the wild population.

This should be done under the supervision of a trained wildlife officer, who will be responsible for collecting detailed records of nest localities and the number of eggs collected. These data, along with hatching records, must be reported to the Department of Wildlife and National Parks. In addition to this, it should be considered mandatory for the crocodiles to be tested for crocodile pox and *Salmonella* infections, amongst others, as a prerequisite to their release. Released crocodiles will be uniquely marked using scute-clipping and, preferably, imbedding PIT units. Furthermore, all animals must be sexed and released based on the required sex ratios. These animals should have some basic morphometric measurements taken prior to release and be released in the nearest deep-water channel to the nest site from which the eggs were removed (except in high disturbance zones), with that locality properly recorded. This will allow the estimation of survival and movement rates of released animals.

REVISING THE QUOTA

Prior to making a decision to increase quotas, the Department of Wildlife and National Parks should take into account:

- Current trends in population size and structure
- Seasonal effects on breeding, recruitment and survivorship
- Any non-commercial mortality events within the population
- Review of previous harvests
- Review of research information

Annual research outputs should be assessed in terms of maintaining precision and accuracy in survey techniques and to adequately monitor population trends. Where modification of scientific protocol is required, this should be discussed and ratified by a panel of scientists, including a representative from the Crocodile Specialist Group, Species Survival Commission, IUCN – The World Conservation Union.

To increase the quota, the DWNP should seek approval from the Ministry of the Environment and the Office of the President, Botswana, with a written quota proposal that provides the rationale for increasing the quota and a summary of relevant information.

If the decision is to decrease the quota, the DWNP need not seek the approval of the above-mentioned parties, but should notify them of their intentions to do so.

In assessing the quota proposal, the Ministry of the Environment will consider whether such revision of the quota is in alliance with the goals and aims of the management plan and whether there is sufficient information presented to justify the change. The use of outside bodies, such as the Crocodile Specialist Group, Species Survival Commission, IUCN - The World Conservation Union, is suggested as an advisory body.

C. LICENSING AND COMPLIANCE

o LICENSING FOR THE COMMERCIAL USE OF THE NILE CROCODILE IN BOTSWANA

In Botswana the Nile crocodile is listed on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). As such, permits and

licensing pertaining to the export, import, movement through Botswana, trade and other commercial use of crocodiles as a resource should conform to the dictates of the convention, as stipulated in the Wildlife Conservation and National Parks Act (1992), Fifth Schedule.

- LICENSE TO HUNT CROCODILES

Nile crocodiles in Botswana are considered game animals, which may be hunted under license (Seventh Schedule, Wildlife Conservation and National Parks Act (1992)). As a game animal without a specific quota assigned to it, a game license may be issued to hunt crocodiles. Landholders' privileges allow a total of 25 crocodiles to be hunted per year (Eighth Schedule, Wildlife Conservation and National Parks Act [1992], Section 20).

It is suggested that in future no crocodiles are removed from the wild in Botswana, unless they are posing a direct threat to human safety or primary production.

- LICENSE TO HARVEST AND SELL CROCODILES AND CROCODILE EGGS

Under the terms of the Wildlife Conservation and National Parks Act section 24 (4):

"Any person granted permission under subsection (1) shall be entitled to farm, ranch, hunt or capture animals on his land, for commercial purposes, subject to the provisions of this section and any terms and conditions subject to which such permission was granted: Provided that protected game animals and partially protected game animals shall only be farmed, ranched, hunted or captured on such land if specifically authorized by the Director."

Under the terms of the Wildlife Conservation and National Parks Act (1992), Section 39:
(1) the Director may, acting in accordance with such directions as may be given by the Minister, grant permits authorizing-

(a) the killing or **capturing** of any animal for the purposes of education or scientific research, providing specimens for museums, zoological gardens and similar institutions, **or the breeding, farming** or domestication of any animal;
(b) the killing or **capturing** of animals in the interests of the conservation, management, control or **utilization of wildlife**; or
(c) the **selling of animals** killed or **captured** under the authority of a license or permit and the selling of any meat, trophy or **eggs** from such animals, where the Director is satisfied that

such selling is in the interests of wildlife conservation and the proper regulation of commercial development connected with wildlife."

(2) The Director shall not grant a permit authorizing the killing or capturing of any animal in a national park, game reserve or sanctuary for any of the purposes mentioned in subsection (1), except only on the ground that and where he is satisfied that, such killing or capturing is necessary for scientific purposes or for the protection of life or property, or in the interests of the conservation, management, control or **utilization of wildlife.**

- LICENSE TO IMPORT / EXPORT CROCODILES AND CROCODILE PRODUCTS

The statutes governing the export, import, transport through and re-export of crocodiles in Botswana are covered in Section 62 of the Wildlife Conservation and National Parks (1992):

Export and Import of Animals, Trophies and Meat and Sale and Manufacture of Articles from Trophies

(1) No person shall, except under and in accordance with the terms and conditions of a permit granted to him by the Director under S.I. 31/1994. subsection (3), export from or import into or transport through or re-export from Botswana any animal, or trophy, meat or eggs thereof.

(2) The export, import, transport through and re-export of animals listed under the Appendices to CITES and any trophy, meat or eggs thereof shall be permitted only in accordance with the provisions of CITES and before any permit is issued under S.I. 31/1994. subsection (3), the Director, as Management Authority in accordance with the terms of CITES, shall require to be satisfied that-

(a) the **animal, trophy, meat or eggs has or have been lawfully acquired**;
(b) **the issue of the permit will not in any way be detrimental to the survival of the species**;
(c) where required, the **Management Authority of the importing country has granted an import permit in respect of the animal, trophy, meat or eggs**; and
(d) **in the case of a live animal, all necessary steps have been taken to minimize the risk of injury, cruelty or damage to its health during transport or transshipment of the animal to its destination.**

(3) Subject to compliance with the provisions of any other written law relating to the export or import of goods, to the provisions of subsections (2) and (4) and to any regulations made or directions given, or terms and conditions imposed by the Minister in respect of certain or specified animals, a licensing officer may, on application being made in such form and on payment of such fee as may be prescribed, **grant permits for the export from or import into or re-export from Botswana of any animal, or trophy, meat or eggs thereof**.

At present, an annual export quota of 4 950 ranched specimens, including live specimens and products and 50 live and trophy animals are permitted by CITES (CITES, 2007).

- REPORTING REQUIREMENTS FOR LICENSES

It is suggested that licensed crocodile farmers and processors are required to submit monthly returns in an approved format. Non-compliance may result in prosecution and/or the cancellation of the relevant license. Licensed ranchers, farmers and trophy hunters should submit license returns at the expiry of their license, which should have a maximum duration of 12 months, but in the case of the removal of problem animals should be issued for the duration of the removal or relocation event.

AIM 3. COMMUNICATION AND EDUCATION

Educating people about the importance of the Nile crocodile both as a “keystone” species within the ecosystem, its value as a tourist attraction and its commercial value is imperative. Once a value is placed on the crocodiles and their direct or indirect benefits to all people in Botswana are made clear, a situation within which their conservation is promoted by the public will arise. This education needs to be approached at a number of levels to be successful, in the form of informative workshops, community meetings and school visits, etc. An excellent example of the promotion of conservation through education is provided by the “Children in the Wilderness” program run through Wilderness Safaris. It is through programs such as this that awareness is initiated and the necessity of conservation made part of society’s knowledge base.

7.1.8 Further recommendations

I. RESEARCH AND REPORTING

It is critical that the DWNP compiles and submits regular reports to CITES in the interests of crocodile management and that these data are updated regularly. At the time that this management plan was written (November, 2007), there were no current reports lodged with CITES regarding *C. niloticus* in Botswana. The reporting of all information regarding the export, import, hunting and research on crocodiles in Botswana would ensure efficient regulation and management and monitoring.

The continuation of research on *C. niloticus* populations both in the Okavango Delta and in other areas in which crocodiles occur in Botswana, such as the Kwando and Chobe Rivers, is required for the ongoing success of this management plan. Research on crocodiles in Botswana should be encouraged and facilitated as far as possible.

II. THE ESTABLISHMENT OF A BREEDING SANCTUARY

- PROPOSED SANCTUARY

A proposal has been submitted to the Tawana Land Board, Maun, for the establishment of a breeding sanctuary for breeding female crocodiles and their nests (Shacks, 2006) in the Lower and Upper Phillipa (also known as "Moremi") Channels (Appendix 3) is being considered by the Tawana Land Board in Maun. As a breeding sanctuary, the law will apply as stipulated in the Wildlife Conservation and National Parks Act (1992), Part II, Section 12.

The Okavango Delta has the Moremi Game Reserve as a protected area, but the ecological significance of the panhandle as the breeding site for Nile crocodiles (and many other species) deserves its' own form of protection. Using the habitat suitability maps (Figure 64, Figure 65**)**, it would make sense to provide the breeding crocodiles with a protected sanctuary. The habitat vulnerability map gives an indication of those areas that are free of any human disturbance and thus forms the base for the selection of a breeding sanctuary area.

Due to the high density of nests in the area and the current low utilization by humans, the Upper (Moremi) and Lower Phillipa channels are ideal nesting sanctuary areas. Regulations that could be implemented include regulated boat access outside of the nesting season, with restricted

access during the breeding season. Proclaiming the area a “no egg collection” zone would ensure that the sanctuary area remains undisturbed. Due to its current accessibility, utilization in this area is still low, however this is expected to change as increased utilization pressure is placed on the ecosystem. This area also includes other rare species threatened by habitat loss such as the African Skimmer and the Wattled Crane.

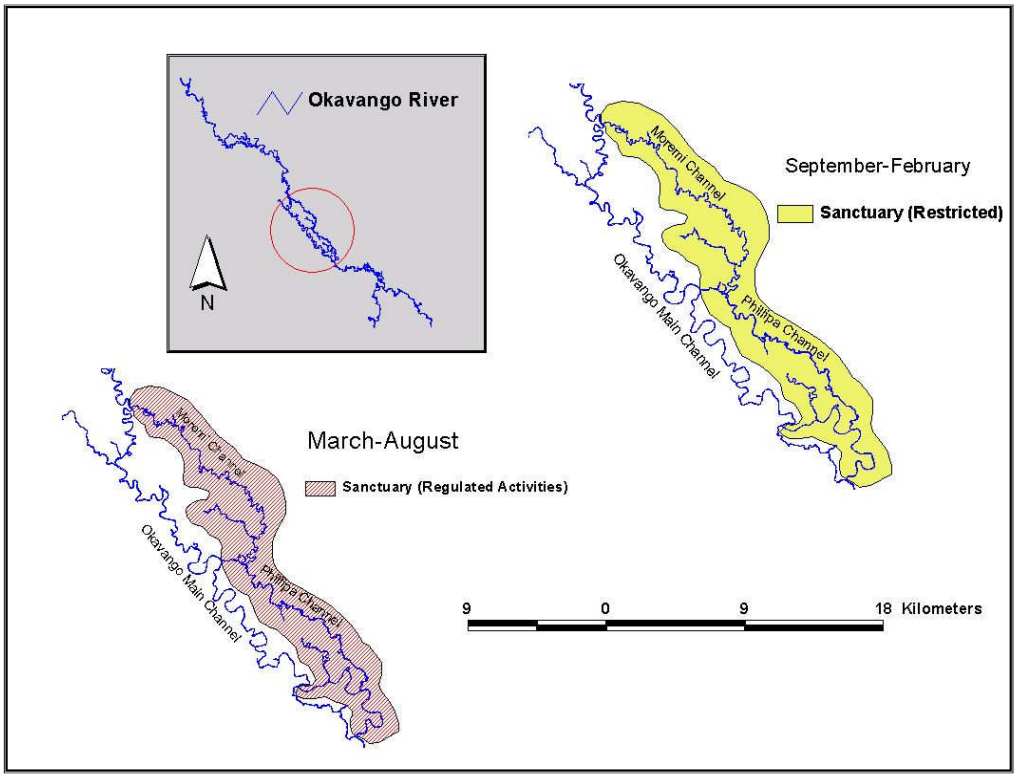

Figure 67. Proposed crocodile nesting sanctuary in the Panhandle region of the Okavango Delta.

The sanctuary could be promoted for regulated tourism during the non-breeding season, which would promote the panhandle as a tourist destination. This sanctuary could also be implemented as part of the Community Based Natural Resource Management (CBNRM) strategy, which aims to protect declining wildlife populations, while devolving greater responsibility to local authorities and communities for management and use of wildlife resources.

The following steps must be taken:

(i) The sanctuary must be ratified as soon as possible after all stakeholders have been consulted.

(ii) The Phillipa sanctuary area must be officially demarcated (3 signs required) and workshops undertaken to provide local villages and lodges with information on the necessity of the sanctuary.

(iii) Law-enforcement procedures must be decided upon with the DWNP (anti-poaching unit) and police officials.

(iv) A strict guideline for activities allowed in the sanctuary area must be decided upon, for example:

a) Only designated members of crocodile monitoring teams have access to the area for monitoring purposes during the restricted time period.

b) During the period of "regulated activities", boats reduce speed so as to avoid wake disturbance and noise disturbance.

c) Throughout the year it becomes illegal to disembark from boats to explore sand banks etc.

It is recommended that the Upper Phillipa and Lower Phillipa Channels (Appendix 3) are designated a sanctuary area under Section 12 of the Wildlife Conservation and National Parks Act (1992). This has been submitted to the Land Board for consideration and the decision regarding the proclamation of the sanctuary is pending.

7.2 CONCLUSION

The Okavango panhandle crocodile population carries a legacy of human-induced perturbation that has reduced its abundance to levels where stochastic events may cause it to be extirpated in the near future. Sound management policies, based on adaptive management strategies, must be implemented if this population is to recover. Sustainable utilization of the crocodiles from this system through commercial ranching may be beneficial to the population, provided these operations are themselves strictly managed. The ratification of a breeding sanctuary is seen as a necessary step towards population recovery. This, combined with the scientific monitoring of the crocodile population, will ensure that this population not only persists, but increases and stabilises in the future.

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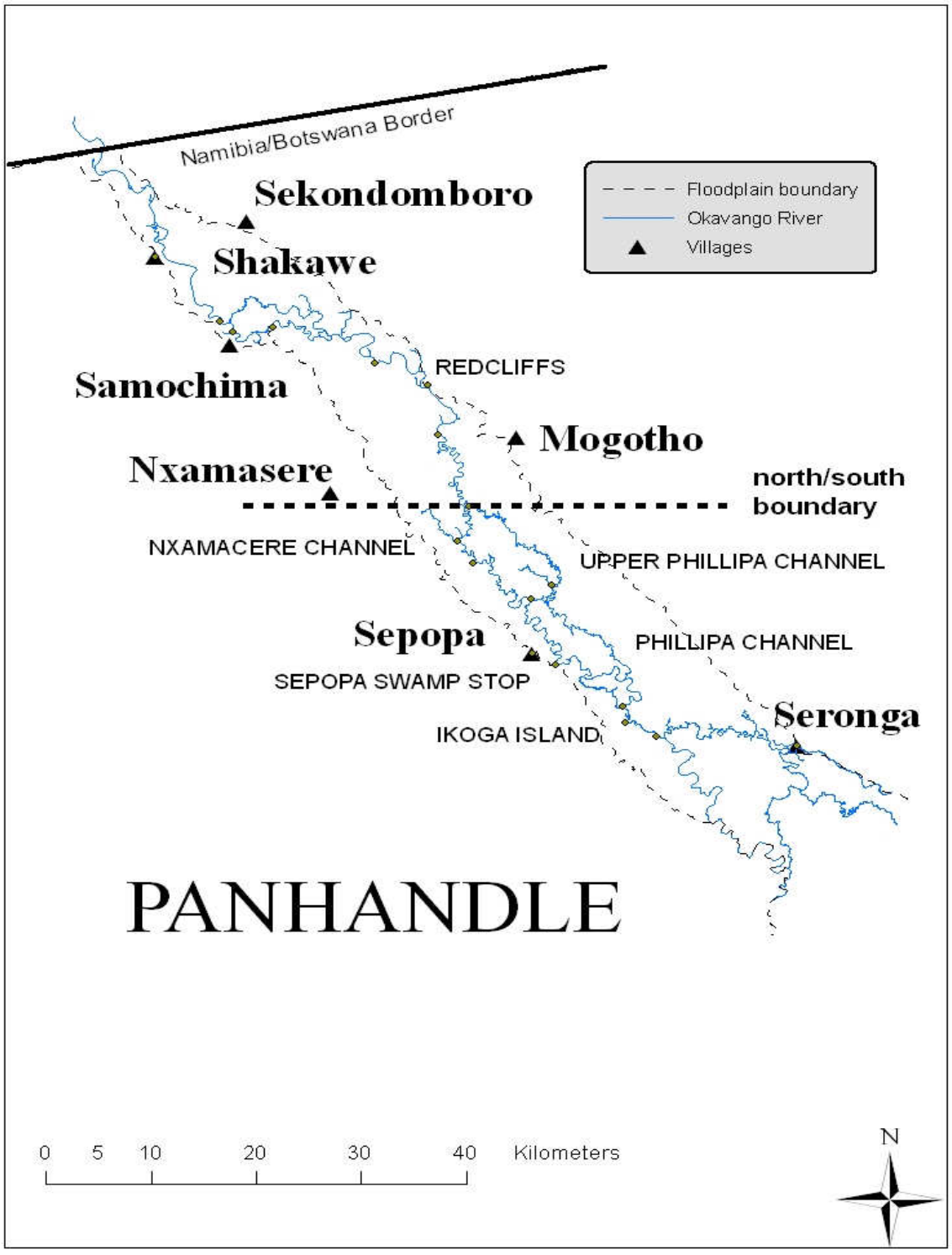
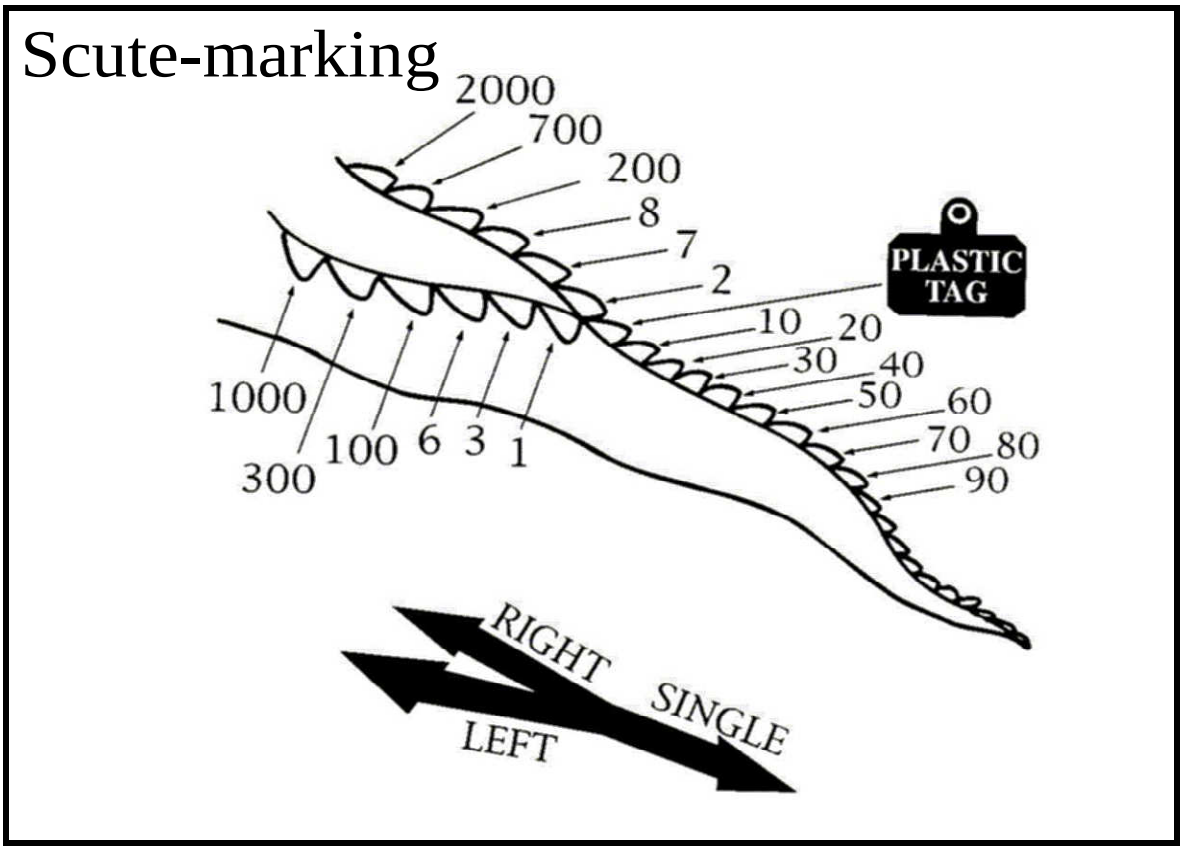
Appendix 3.The panhandle region of the Okavango Delta, Botswana, showing the extent of the study area and the delineation (dotted line) between the "northern" and "southern" research areas.



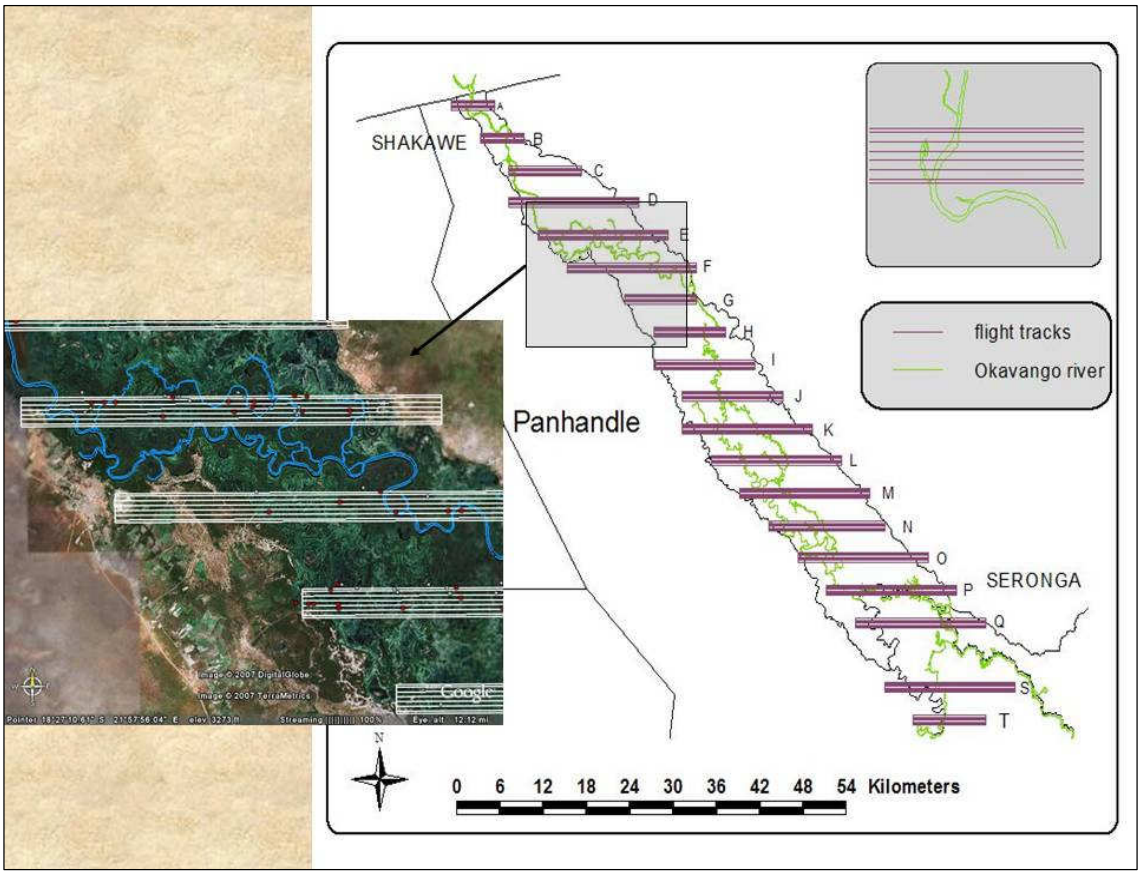
Appendix 4. Diagrammatic illustration of the scute-removal method. Scutes corresponding or adding up to individual crocodile's allocated number are removed with a sterile surgical scalpel (Leslie, 1997).



Appendix 5. The pitman noose trap, set with bait (top) and with large adult male trapped (bottom).

Appendix 5 (cont.). The Box trap, set with bait (top) and containing a captured adult (bottom).

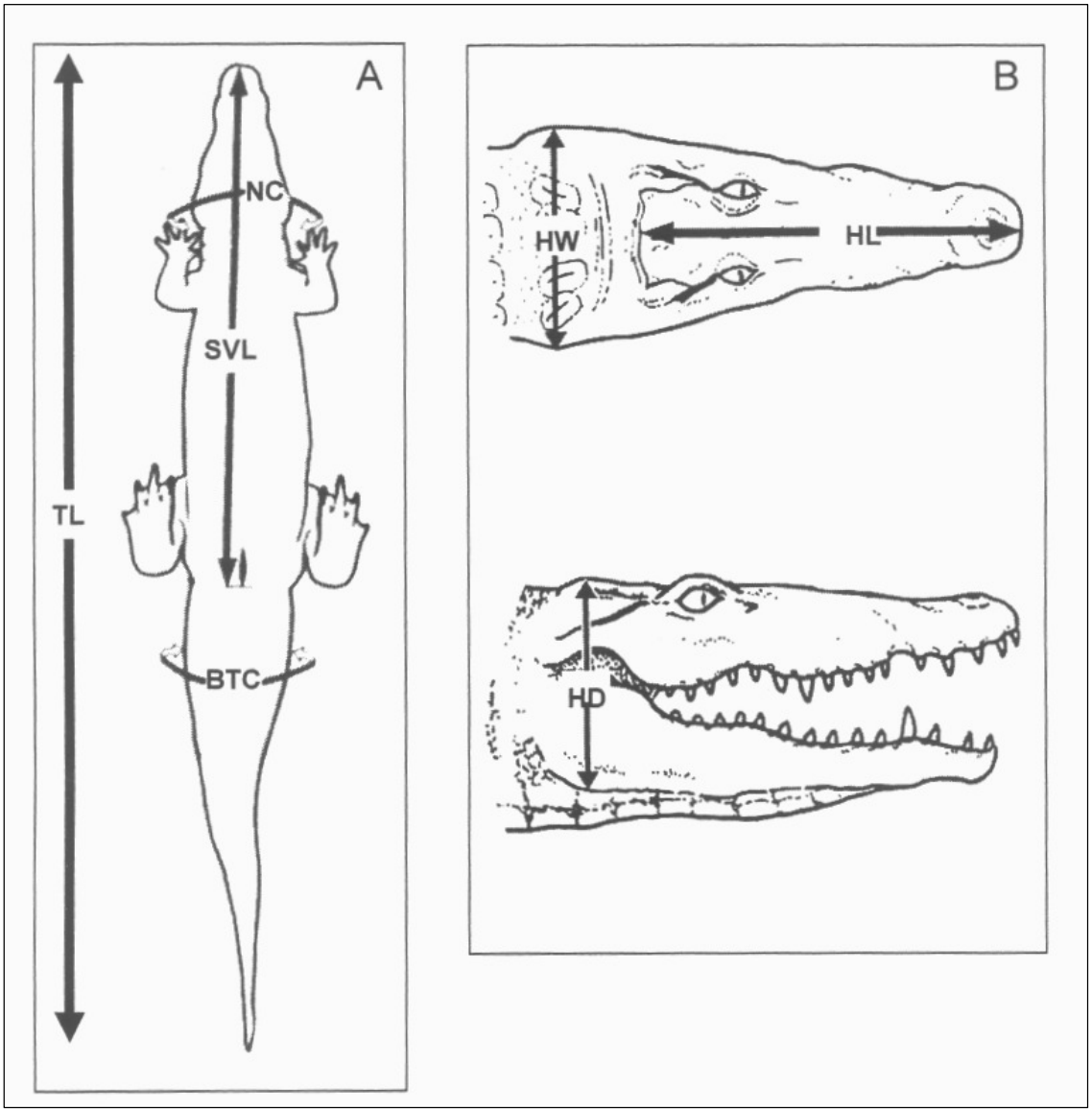
Appendix 6. A diagram showing the flight tracks used during the aerial surveys, crossing panhandle floodplain in an east-west orientation. Within each block there are six flight tracks, spaced at 200 m intervals. Total counts were conducted in each block.



Appendix 7. Schematic diagram of morphometric measurements recorded from each captured crocodile for (A) body and (B) head (Leslie, 1997).

Diagram A: TL = total length, SVL = snout-vent length, NC = neck circumference, BTC = base of tail circumference.

Diagram B: HL = head length, HW = head width, HD = head depth.



Appendix 8. Theses, publications, reports, seminars, workshops and public articles generated by the Okavango Crocodile Research Group from 2002 - 2006

Theses

- Bourquin, S.L. (Submitted). The Population Ecology of the Nile Crocodile, *Crocodylus niloticus*, in the Okavango Delta, Botswana. PhD Thesis, University of Stellenbosch, South Africa.
- Detoeuf-Boulade, A.S. (2006). Reproductive cycle and sexual size dimorphism of the Nile crocodile (*Crocodylus niloticus*) in the Okavango delta, Botswana. MSc Thesis, University of Stellenbosch, South Africa.
- Lovely, C. (2007). The Nile crocodiles of the Okavango Delta in Health and Disease. MSc Thesis. University of Stellenbosch, South Africa.
- Maciejewski, K. (2006). Temperature-Dependant Sex Determination in the Nile Crocodile *Crocodylus niloticus* in the Okavango River, Botswana and the Effect of Global Climate Change. MSc Thesis, University of Stellenbosch, South Africa.
- Mengdehl, C. (2004). Phenotypic Plasticity of the Liver and Small Intestine of the Nile Crocodile (*Crocodylus niloticus*) in the Wild Population of the Okavango River, Botswana. MA Thesis, University of Jena / University of Stellenbosch.
- Shacks, V.A. (2006) Habitat vulnerability for the Nile crocodile (*Crocodylus niloticus*) for the Okavango Delta, Botswana. MA Thesis, University of Stellenbosch, South Africa.
- Thomas, G.D. (2006) Human-crocodile conflict (Nile crocodile: *Crocodylus niloticus*) in the Okavango Delta, Botswana. MSc Thesis, University of Stellenbosch, South Africa.
- Wallace, K.M. (2006). The Feeding Ecology of Yearling, Juvenile and Sub-adult Nile Crocodiles (*Crocodylus niloticus*) in the Okavango Delta, Botswana. MSc Thesis, University of Stellenbosch, South Africa.

Publications

- Smit, N.J., Leslie, A. & Davies, A.J. (2005). The Protozoan Blood Parasites of the Nile Crocodile, *Crocodylus niloticus*, from the Okavango Delta, Botswana. *Journal of the South African Veterinary Association*,76, 182-183.
- Gomersall, D.P., Smit, N.J. & Leslie, A. (2006). Prevalence, Distribution and Possible Vector of *Hepatozoon pettiti*, Blood Parasite of Nile Crocodiles in the Okavango Delta. *Journal of the South African Veterinary Association*, 77, 93-96.

- Junker, K., Wallace, K., Leslie, A.J. & Boomker, J. (2006). Gastric Nematodes of Nile Crocodiles, *Crocodylus niloticus*, Laurenti, 1768, in the Okavango River, Botswana. *Onderstepoort Journal of Veterinary Research*, **77**, 111-114.
- Lovely, C., Pittman, J.M. & Leslie, A.J. (in Press) Normal Haematology and Blood Chemistry of Wild Crocodiles (*Crocodylus niloticus*) in the Okavango Delta, Botswana. *Submitted to the Journal of The South African Veterinary Association.*
- Gomersall, D.P., Smit, N.J., Oosthuizen, M.C., Penzhorn, B.L. & Leslie, A. (in Press). Molecular Phylogenetic Analysis of Crocodilian Blood Protozoans of the Genus Hepatozoon. *Journal of the South African Veterinary Association.*
- Gomersall, D.P., Smit, N.J. & Leslie, A. & Davies, A.J. (in Prep) Prevalence and Distribution of *Hepatozoon petteti* (Apicomplexa: Adeleorina: Haemogregarinidae) Infecting Nile Crocodiles (*Crocodylus niloticus*) from the Okavango Delta, Botswana. *Submitted to Journal of Parasitology.*
- Gomersall, D.P., Smit, N.J., Oosthuizen, M.C., Penzhorn, B.L. & Leslie, A.J. (in Press) Molecular Phylogenetic Analysis of Crocodilian Blood Protozoans of the Genus Hepatozoon. *Journal of the South African Veterinary Association.*
- Wallace, K.M. & Leslie, A.J. (in Press). The Diet of the Nile Crocodile (*Crocodylus niloticus*) in the Okavango Delta, Botswana. *Journal of Herpetology.*
- Bishop, J., Leslie, A.J., Bourquin, S.L., & O'Ryan, C. (in Press). Overexploitation and the Declining Effective Population Size of a Top Predator. *Submitted to Proceedings of the Royal Society Bulletin, London.*

Seminars

- Leslie, A.J. 2002. Crocodiles of the Okavango. Royal Geographic Society of London, Invited speaker. May 2002.
- Leslie, A.J. 2002. Crocodiles of the Okavango. Harry Oppenheimer Okavango Research Centre, University of Botswana, Maun. Seminar series, September 2002.
- Leslie, A.J. 2003. Okavango's Crocodiles. Department Zoology, University of Cape Town. Invited speaker. May 2003.
- Leslie, A.J. 2003. Ecology, Physiology and Conservation of the Nile crocodile, *Crocodylus niloticus*, in the Okavango delta, Botswana. Wildlife Management Association of Southern Africa, Ganzekraal, South Africa, 21-23 September 2003. Oral presentation.
- Leslie, A.J. 2003. Okavango's Crocodiles. Earthwatch Principal Investigators Symposium, Cambridge, Massachussetts, USA. 5-9 November 2003. Invited Speaker.

- Leslie, A.J. 2003. Okavango's Crocodiles. Harvard Travellers Club, Boston USA. 11 November 2003. Invited Speaker.
- Leslie, A.J. 2003. Okavango's Crocodiles. Parthenon Dinners Club, Chicago, USA. 9 November 2003. Invited Speaker.
- Leslie, A.J. 2003. The Okavango Story. National Zoological Gardens, Washington DC, USA. 15th November 2003. Invited Speaker.
- Leslie, A.J. 2004. Okavango's Crocodiles. Workshop Presentation for the Department of Wildlife and National Parks, Maun, Botswana.
- Smit, N.J., Leslie, A.J & Davies A.J. 2004. Protozoan Blood Parasites of the Nile crocodile, *Crocodylus niloticus*, from the Okavango Delta, Botswana. Poster Presentation. 33 rd Annual Conference of PARSA (Parasitological Association of Southern Africa), 12 - 15 September, Manyane, Pilanesberg National Park, North West Province, South Africa.
- Thomas, G.D. &. Leslie, A.J. 2004. Human / Crododile Conflict in the Okavango Delta, Botswana. 7th Symposium of the Herpetological Association of Africa (HAA), Port Elizabeth, October 2004.
- Bourquin, S.L. & Leslie, A.J. 2004. Population Ecology of the Nile Crocodile in the Okavango Delta, Botswana. 7th Symposium of the Herpetological Association of Africa (HAA), Port Elizabeth, October 2004.
- Leslie, A.J. 2004. The Okavango Story. Somerset-West Wildlife Society, Western Cape, South Africa. Invited speaker.
- Leslie. A.J. 2005. Ecology, Physiology and Conservation of the Nile Crocodile, *Crocodylus niloticus*, in the Okavango delta, Botswana. Kalahari Conservation Society (KCS) Annual Symposium, Gaborone, Botswana. Invited speaker.
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Workshops

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Productions

- "Womans Hour", Channel 4, BBC Radio, London, 2003.
- National Geographic Television. Crocodile Chronicles. "Beasts of Botswana", Premiered February 2003
- Tigress productions (UK) film shoot. Botswana's crocodiles. June 2003.
- Gedeon Programmes, Paris, France. "The Monster of Tanganyika". A crocodile special. Premiered January 2004.

- EarthBound 3. Okavango's crocodile team. John Hemmingway Film productions. 2004.
- Strings Productions. "Okavango Crocodiles" for 50 / 50. March 2004.
- Tierzight Productions, Germany. Okavango's crocodiles. 2005.
- Kyknet Television Show, South Africa. April 2005.

Popular articles

- African Wildlife. May/June 2001. "New Research into the Okavango's Gently Smiling Jaws"
- Ngami Times, Maun, Botswana. "Launch of the Okavango Crocodile Project". January 2002.
- Marung Magazine. Air Botswana. "Botswana's gently Smiling Jaws". May 2002.
- Global Adventure Travel. Okavango's Crocodiles. July 2002.
- Travel Africa Magazine. Summer 2003. Top 50 things to do in Africa: Crocodile Research.
- Tim Neary radio talk show host. Radio 702 and Radio SA FM. June 2003.
- Crocodile Specialist Group Newsletter, Crocodile project update Vol 23 No. 4. 2004.
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